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Cladistics and polychaetes

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A series of cladistic analyses assesses the status and membership of the taxon Polychaeta. The available literature, and a review by Fauchald & Rouse (1997), on the 80 accepted families of the Polychaeta are used to develop characters and data matrices. As well as the polychaete families, non-polychaete taxa, such as the Echiura, Euarthropoda, Onychophora, Pogonophora (as Frenulata and Vestimentifera), Clitellata, Aeolosomatidae and Potamodrilidae, are included in the analyses. All trees are rooted using the Sipuncula as outgroup. Characters are based on features (where present) such as the prostomium, peristomium, antennae, palps, nuchal organs, parapodia, stomodaeum, segmental organ structure and distribution, circulation and chaetae. A number of analyses are performed, involving different ways of coding and weighting the characters, as well as the number of taxa included. Transformation series are provided for several of these analyses. One of the analyses is chosen to provide a new classification. The Annelida is found to be monophyletic, though weakly supported, and comprises the Clitellata and Polychaeta. The Polychaeta is monophyletic only if taxa such as the Pogonophora, Aeolosomatidae and Potamodrilidae are included and is also weakly supported. The Pogonophora is reduced to the rank of family within the Polychaeta and reverts to the name Siboglinidae Caullery, 1914. The new classification does not use Linnaean categories, and the Polychaeta comprises two clades, the Scolecida and Palpata. The Palpata has the clades Aciculata and Canalipalpata. The Aciculata contains the Phyllodocida and Eunicida. The Canalipalpata has three clades; the Sabellida (including the Siboglinidae) Spionida and Terebellida. The position of a number of families requires further investigation. © 1997 The Norwegian Academy of Science and Letters.

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Contents

Introduction

Rouse & Fauchald (1995) cast doubt on the monophyly of the traditionally formulated Annelida. They applied the name Articulata to the clades Clitellata, Euarthropoda, Onychophora, Pogonophora (= Frenulata and Vestimen-

tifera) and Polychaeta. A major assumption in that analysis was the monophyly of the Polychaeta, a taxon that has never been identified by apomorphy. This was not particularly problematic in the context of that paper and in fact allowed Rouse & Fauchald (1995: 294) to conclude that "the Clitellata, 'arthropods', and Pogonophora may

well prove to fall inside the Polychaeta; use of these taxa as outgroups for an analysis of polychaete relationships is not justifiable at this time".

The history of the taxon Polychaeta was reviewed in detail by Fauchald & Rouse (1997), along with a summary of the various taxa at the family level and of morphological features that have been used to classify the group. Fauchald & Rouse (1997) found that 80 families currently (or usually) placed in the Polychaeta should be considered in any phylogenetic analysis at that taxonomic level. Additionally, based on discussion and results of Rouse & Fauchald (1995) and Fauchald & Rouse (1997), the status of current non-polychaete groups, such as the Aeolosomatidae, Clitellata, Euarthropoda, Frenulata, Onychophora, Potamodrilidae and Vestimentifera, should be considered in any analysis of the Polychaeta.

The aims of this paper are several:

1. To assess the monophyly of the Polychaeta and relationships among the taxa usually included in the group and those traditionally excluded.

2. To provide a new classification.

3. To discuss the possible transformation of characters used in the study.

Proposing a new classification is somewhat problematic since this study is a first heuristic step in terms of bringing polychaete systematics to an acceptable level of rigour. Any classification proposed is unlikely to have any longevity because of the inadequate knowledge of many taxa. However, the current situation is untenable, so what is presented must be considered an improvement. Various issues of character coding and weighting are explored since these are fundamental to any cladistic analysis.

Methods

Taxa considered

Rouse & Fauchald (1995) identified the Echiura as the sister group to the Articulata, which comprises the Clitellata, Euarthropoda, Onychophora, Polychaeta, and Pogonophora (= Frenulata and Vestimentifera). It has been postulated by Nielsen (1995) and Eibye-Jacobsen & Nielsen (1996) that the Echiura are polychaetes that have secondarily lost all signs of segmentation and should a priori be included in this taxon. While there is virtually no evidence to support this assumption, it is tested here by including the Echiura as part of the ingroup and rooting the cladograms using the Sipuncula. Rouse & Fauchald (1995) indicated that either the Sipuncula or Mollusca, or both as a clade, could be regarded as sister group to the Echiura plus Articulata clade. The Sipuncula is selected here as the outgroup. Apart from the echiurans, the Onychophora, Euarthropoda, Frenulata, Vestimentifera, Clitellata and all polychaete families are considered in this study. The position of a number of purported non-polychaete taxa such as the Aeolosomatidae and Potamodrilidae that were excluded from the analysis of Rouse & Fauchald (1995) is also assessed.

Polychaete families are used as terminal taxa largely because this allows the most heuristic assessment of relationships based on present knowledge, and also permits many of the current problems in the systematics of polychaetes to be highlighted. Problems with coding families as terminal taxa are discussed below. Classifications of polychaetes above the level of family were reviewed in Fauchald & Rouse (1997) and found to be unsatisfactory for cladistic analysis. Attempting any analyses below the family level, say at 'species' level, is beyond the scope of this study, in terms of computational capabilities, time and available information.

Taxa excluded from the restricted analyses. In many cases, polychaete groups have been given the status of family more for their unusual mode of existence rather than proper consideration of their systematic placement. This was effectively demonstrated by Westheide (1985) and

Eibye-Jacobsen & Kristensen (1994) for the Dorvilleidae, which is paraphyletic if the Dinophilidae (interstitial/minute) and Iphitimidae (commensals with crustaceans) are recognised. This paper has a series of analyses where all polychaete families that can be classified as being symbiotic (*sensu lato*), pelagic or interstitial were excluded. It is likely that many of the families excluded from the restricted analyses will prove to make other taxa paraphyletic. This is not to suggest that all the families included in the restricted analyses are monophyletic; this is probably very far from the truth. The use of paraphyletic taxa is not problematic in cladistic analyses and is a common occurrence (Rouse 1996). In general, paraphyletic taxa will appear as the sister group to their excluded members. However, the mode of existence of most of the 29 excluded taxa is such that many of the features that they have probably lost, such as chaetae, would have to be coded as absent and would appear as such in the resulting trees. This could possibly, though not necessarily, complicate the analyses and give misleading results. Four families were also excluded because they are insufficiently known. All taxa are, however, scored and documented in the Appendices. Analyses including all 80 accepted polychaete families (and the Aeolosomatidae and Potamodrilidae) are also shown for the various forms of character coding.

The excluded taxa are grouped into several categories:

(A) Symbiotic (= commensal/parasitic) taxa. The assumption here is that any symbiotic group of polychaetes is derived from a free-living group. Parasitic organisms are known for their apomorphic features often combined with apparent morphological simplicity (Brooks & McLennan 1993). Depending on the level of analysis chosen, this latter condition can appear as an absence rather than a loss and hence can seriously affect tree topologies. All parasitic or commensal polychaete families are excluded owing to this possibility. Cladistic placement has been hypothesised for most of them and should be assessed in more restricted analyses where more relevant characters can be used to assess relationships. In the context of this study, the inclusion of most of the symbiotic groups is trivial. The excluded families in this category are:

(1) *Histriobdellidae.* Parasitic/commensal on crustaceans. Probable sister group among taxa with a hypertrophied ventral proboscis (see Jamieson *et al.* 1985).

(2) *Ichthyotomidae.* Parasitic on anguilliform teleosts. Probable sister group among taxa either with a hypertrophied axial proboscis or hypertrophied ventral proboscis (Fauchald 1977; Pettibone 1982).

(3) *Myzostomidae.* Parasitic/commensal on echinoderms. Recent studies on the myzostomids have all indicated that they should be regarded as a group of polychaetes (see review in Rouse & Fauchald 1995). Rouse & Fauchald (1995) proposed that myzostomids probably have a sister group among taxa having a hypertrophied axial proboscis.

(4) *Nautilliennellidae.* Parasitic/commensal of bivalves. Found to be either the sister group to the Pilargidae or Syllidae (Glasby 1993).

(5) *Oenonidae.* In most cases, there is a parasitic phase of life cycle in other polychaetes. Sister group among taxa with a hypertrophied ventral proboscis.

(6) *Spintheridae.* 'Parasitic' on sponges, probable sister group in the amphinomid/euphrosinid clade.

(B) Pelagic taxa. While there is no real evidence to support the hypothesis, all pelagic polychaete taxa are assumed to be derived from benthic ancestors. Their status as families should be carefully assessed, and it would appear that many of the features that they lack may be attributable to losses associated with a pelagic existence rather than being primitive. Pelagic polychaete families are:

(7) *Alciopidae.* Often treated as a subfamily of the Phyllodocidae and score identically to this taxon in this study.

(8) *Iospilidae.* Little is known about this group, and further anatomical study is required.

(9) *Lopadorhynchidae.* Often treated as a subfamily of Phyllodocidae (Uschakov 1955; Day 1967) and clearly in need of further investigation.

(10) *Poeobiidae.* The single species in this family, *Poeobius meseres*, is one of the few achaetous polychaetes and has had a varied taxonomic history. Detailed morphological studies have stabilised it as a polychaete group sharing many features with flabelligerids. The discovery of pelagic 'flabelligerids' such as *Flota flabelligera* Hartman, 1967 (placed in Fauveliopsidae by Hartman 1971, *incertae sedis* according to Fauchald 1977 and in the Flotidae by Buzhinskaja, 1996) that are similar to *Poeobius* suggests that recognition of the Poeobiidae makes the Flabelligeridae paraphyletic, and that they should be included in any cladistic analysis of this family, as should any of the Fauveliopsidae (*sensu* Hartman 1971).

(11) *Pontodoridae.* Though considered part of the suborder Phyllodociformia by Fauchald (1977), the presence of a proventricle actually suggests that a relationship with the Syllidae should be investigated (see Day 1967: 167).

(12) *Tomopteridae.* The unusual morphology of this group means that, although they seem related to taxa with a hypertrophied axial proboscis, the current level of study would provide spurious results.

(13) *Typhloscolecidae.* Same comments as for Tomopteridae.

(C) Interstitial (or small) taxa. The small size of most interstitial taxa has been linked to simple body forms. While not wishing to promote any hypotheses concerning the size of plesiomorphic polychaetes or annelids, most of the taxa excluded arguably have larger sister taxa (see Westheide 1985,1997). Excluded interstitial families are:

(14) *Aeolosomatidae.* A largely freshwater group that has never been placed in the Polychaeta. Their position is considered, but they are left out of the restricted analyses because of their extremely small size and simple morphology.

(15) *Ctenodrilidae.* A relationship with the Cirratulidae was originally postulated by Mesnil & Caullery (1897). The several ctenodrilid genera should be considered in any cladistic analysis of Cirratulidae.

(16) *Diurodrilidae.* A genus of very small species that were originally placed in the Dinophilidae by Remane (1932). *Diurodrilus* was placed in its own family by Kristensen & Niilonen (1982). *Diurodrilus* should possibly have been included by Eibye-Jacobsen & Kristensen (1994) in their cladistic analysis of the Dorvilleidae. In not doing so, the latter may still be paraphyletic.

(17) *Fauveliopsidae.* While not strictly interstitial, they are listed here because of their relatively small size. Usually considered to be close to, or as members of, the Flabelligeridae (McIntosh 1922; Hartman 1967,1971), they were placed in their own order by Fauchald (1977). Detailed examination of the internal anatomy is required to assess their original placement by McIntosh (1922). As mentioned above for the Poeobiidae, taxa in the Fauveliopsidae should be assessed in relation to the Flabelligeridae.

(18) *Nerillidae.* The placement of this group is problematic. The structure of the head, and presence of compound chaetae in some taxa, suggests a probable sister group among taxa either with a hypertrophied axial proboscis or hypertrophied ventral proboscis.

(19) *Parergodrilidae.* The morphological simplicity and the lack of essential information for this group mean that their placement is unresolvable at present.

(20) *Polygordiidae.* A group considered to be closely related to the Saccocirridae and Protodrilidae (Goodrich 1901) and hence probably close to spiomorph taxa (Purschke & Jouin 1988).

(21) *Potamodrilidae.* Erected by Bunke (1967) for a genus originally within the Aeolosomatidae, the placement of this group is problematic given their small size and lack of comparable features with other ingroup taxa.

(22) *Protodrilidae.* Considered to be closest to spiomorphs by Purschke & Jouin (1988).

(23) *Protodriloididae.* Considered to be closest to spiomorphs by Purschke & Jouin (1988).

(24) *Psammodrilidae.* The placement of this group is unresolved and deserves close study. Bartolomaeus (1995) suggested a relationship with polychaetes having hooks, such as the Maldanidae and Arenicolidae.

(25) *Saccocirridae.* Considered to be closest to spiomorphs by Purschke & Jouin (1988).

(D) Poorly known taxa. The following four families were excluded on the basis of insufficient knowledge:

(26) *Aberrantidae.* The morphology and systematic placement of this group is under investigation and will be reported elsewhere (Mackie *et al.*, in prep.).

(27) *Hartmaniellidae.* Based on the pharyngeal structures, this is clearly a eunicemorph group, otherwise placement is unresolved.

(28) *Sternaspidae.* While the internal anatomy has been studied, there has been very little resolved in terms of the placement of this group. Examination of their anterior ends for any palpal structures is required since they have potentially been reported in one species of *Sternaspis* (Sluiter 1882).

(29) *Uncispionidae.* Though clearly a spiomorph group, the uncispionids are so poorly known that including them would serve no real purpose in this study.

Some taxa would appear to render other families paraphyletic, e.g. the Alvinellidae and Pholoidae making the Ampharetidae and Sigalionidae paraphyletic, respectively. It is also possible that the Pholoidae represents a polyphyletic assemblage drawn from the Sigalionidae. A cladistic analysis of the Sigalionidae and Pholoidae is required to resolve the situation. However, the Pholoidae are included in the restricted analyses since other scaleworm taxa are problematic in terms of monophyly, and the whole group needs revision. The results of Féral *et al.* (1994) suggest that the Terebellidae is paraphyletic if the Alvinellidae is recognised, though they were originally described as ampharetids. The alvinellids are included in the restricted analyses to assess this hypothesis.

Taxa excluded completely. The taxa Gnathostomulida, Lobatocerebridae or the genus *Jennaria* are not included in any analysis. Reasons for the exclusion of the latter two taxa are outlined in Rouse & Fauchald (1995: 274). Exclusion of the Gnathostomulida is based on the lack of evidence supporting Nielsen's (1995) placement of them in the Polychaeta. Further

study on this enigmatic group is clearly required. Various polychaete families are not considered in this study because they quite clearly belong within other families or they were too poorly described initially. These taxa are discussed in Fauchald & Rouse (1997).

Scoring of taxa

Each score for every taxon is documented in Appendix IV. This documentation is largely based on primary sources, but standard reviews such as Rullier (1951) for nuchal organs and lateral organs, were used when the information was uncontroversial. Cases of disagreement among different literature sources are discussed in Appendix IV. There were two alternatives for coding the families for this study. Conducting an analysis of representatives of species from each of the families, say the 'type' species of the 'type' genus, has the advantage that assumptions do not have to be made about the plesiomorphic condition for a family, or whether it is monophyletic. This approach was used by Fitzhugh (1989) for sabellids as a heuristic first step, and subsequently, he has followed this up with detailed analysis at the species level, resulting in major revisions (e.g. Fitzhugh 1993). This is probably the better way to approach a family level analysis as well, since coding a 'family' is fraught with problems largely to do with assessing the plesiomorphic state for the taxon. However, this was not feasible here, partially because of the wide range of characters that were considered and because the type species of each family have often been poorly studied. Assessments were therefore made of the possible plesiomorphic condition for each character for the taxa concerned (Yeates 1995). In most cases, the variability of a given feature across a family is trivial and presented few problems. Where a cladistic analysis was available for a taxon, e.g. Nereididae (Fitzhugh 1987), Phyllodocidae (Pleijel 1991), Sabellidae (Fitzhugh 1989), then a plesiomorphic state for many of the characters involved could be assessed. Often, information was only available for one species in a family, and this had to be used in isolation. This is particularly the case for internal anatomical features. Much of the detail concerning characters and polychaete morphology can be found in Fauchald & Rouse (1997) and is not repeated here. What is made clear by the reviews of the families as a whole in both Fauchald & Rouse (1997) and Appendix IV is that the majority of polychaete groups, in particular many of the recently erected families, have been very poorly studied. Much of the most detailed work can be dated back to the last century, and it would seem that there has been much less emphasis on detailed studies of polychaete morphology in the 20th century. This may be accounted for by the influence of workers more concerned with the taxonomy of polychaetes rather than polychaete systematics.

Characters

The major morphological features of polychaetes were reviewed in detail in Fauchald & Rouse (1997). The outline of the morphological variation described in that review provides the basis for character and state delimitation provided here. A proper assessment of the scoring and results provided here thus requires consultation of Fauchald & Rouse (1997) and Appendix I, Appendix II, Appendix III and Appendix IV. Appendix IV provides the basis for all the scoring in the matrices (Appendix II) and is to be taken as the primary source if there are any discrepancies with Fauchald & Rouse (1997). Virtually all scores are documented by a reference and illustration, usually from the original literature. As an aid for understanding the character states, a number of figures have been provided here that illustrate the major features of polychaete morphology. Where uninformative states have been coded, the feature is generally not figured, as are a number of 'minor' morphological features.

Head. Characters relating to the head involve the prostomium, peristomium, palps and antennae.

Prostomium. Clearly demarked by a distinct groove (Figs 2–6, 8, 8–10, 15, 16); fused to the peristomium and limited (Figs 11, 13, 14); on peristomium, frontal edge fused to peristomium (Figs 1, 17).

Peristomium. Forms a distinct ring (Figs 10, 11); forms two distinct rings (Fig. 6); elongate (Fig. 15); forms rings and a collar (Fig. 14); limited to lips only (Figs 5, 16).

Palps and antennae. Prostomial antennae (Figs 2, 6, 8, 12, 31, 32).

Prostomial grooved palps paired (Fig. 11); multiple (Fig. 17); form a crown (Fig. 14). Peristomial grooved palps paired (Figs 4, 7, 13, Figs 15, 16); multiple (Fig. 1). Prostomial (sensory) palps ventral (Figs 8, 12, 32); ventro-lateral (Figs 2, 6).

External body structures.

First segment. Indistinct or foreshortened (Fig. 8); similar to those following (Figs 6, 9, 10, 14); surrounds head (Fig. 12); fused to head (Figs 13, 17); dorso-lateral around head (Fig. 2); elongate (Fig. 15). First segment appendages same as following (Figs 6, 9); appendages/chaetae

absent (Figs 1, 3, 5); tentacular cirri only (Fig. 8); with notopodia only (Fig. 14). Tentacular cirri (Figs 8, 12).

Parapodia. With similar rami (Fig. 18); with projecting neuropodia (Fig. 20); with tori (Fig. 19); in part notopodial ridges (Fig. 22); spioniform (Fig. 23). Dorsal cirri typically cirriform (Figs 8, 12, 31); include elytra (Fig. 12); foliaceous (Figs 21, 34). Ventral cirri (Figs 18, 20, 22).

Gills. Parapodial branchiae (Figs 6, 9, 18); dorsal simple branchiae (Fig. 4); dorsal flattened branchiae (Figs 13, 23); dorsal branchiae in a few anterior chaetigers (Figs 1, 17).

Internal anatomy.

Stomodaeum. Axial hypertrophied (Figs 24, 31–33); ventral buccal bulb (Fig. 27); ventral hypertrophied (Fig. 26); axial simple (Fig. 25).

Axial hypertrophied stomodaeum. With one lateral pair of jaws (Fig. 32); one or two dorso-ventral pairs of jaws (Fig. 24); with jaws forming a cross or circle (Fig. 33); with jaws forming a single tooth (Fig. 31); with jaws absent (Fig. 34); with a proventricle (Fig. 31).

Ventral hypertrophied stomodaeum. Jaws ctenognath (Fig. 35); prionognath (Fig. 36); labidognath (Fig. 37).

Gular membrane and gut. Gular membrane present (Fig. 25). Gut with lateral folds (Fig. 30); with side branches (Fig. 29); a straight tube (Fig. 28).

Segmental organs. Adult nephridia metanephridia (Figs 40, 41); protonephridia (Figs 38, 39). Nephridia and mesodermal elements form mixonephridia (Figs 43–45); metanephromixia (Figs 40–42); protonephromixia (Figs 38, 39).

Circulation. Closed circulatory system (Fig. 5); heart body (Fig. 5).

Chaetae. Chaetal inversion (Fig. 14); aciculae (Fig. 20); compound chaetae with two ligaments (Fig. 50); compound chaetae with one ligament (Figs 46–48); compound chaetae with a fold (Fig. 49); compound chaetae tapered (Fig. 46); compound chaetae falcate (Fig. 47); compound chaetae dentate (Fig. 48); compound chaetae hooked (Fig. 49); capillary chaetae (Fig. 51); spines (Fig. 52); spines in one anterior chaetiger (Fig. 13); hooded chaetae (Fig. 53); dentate hooks (Fig. 54); uncini (Fig. 55).

Coding issues

As briefly discussed by Rouse & Fauchald (1995), current computer programs for cladistic analysis restrict the use of characters that are nested. The requirement that characters be 'independent' has often been ignored with misleading results (see Rouse & Fauchald 1995). Recently, the problems with character coding have been addressed by several
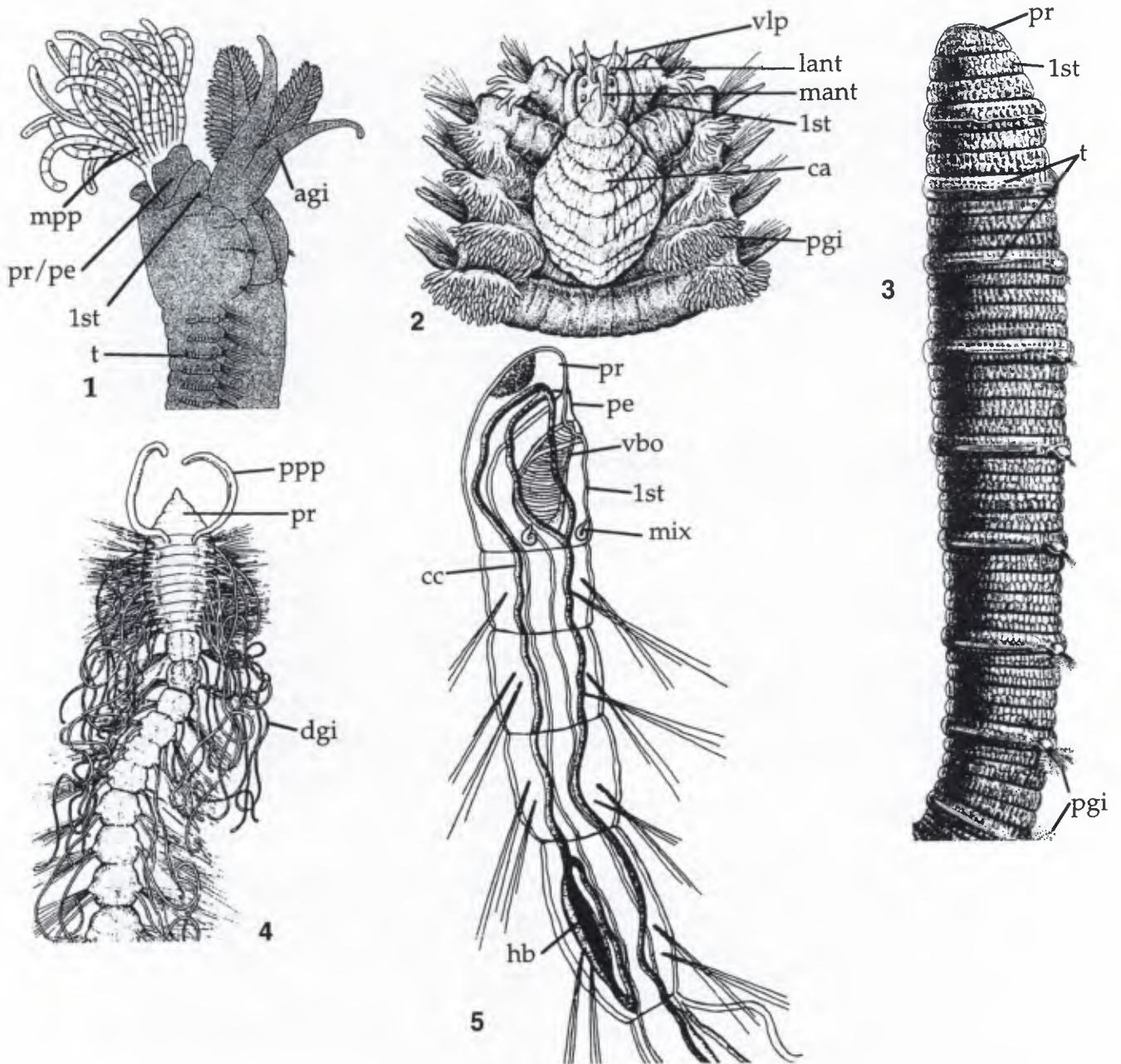
Figs 1–5. Polychaete anterior ends.—1. Lateral view of anterior end with tentacles fully extruded (gills on right side omitted) *Isolda pulchella* (Ampharetidae) (modified from Day 1967: fig. 35.1.k).—*2.* Dorsal view of *Hermodice carunculata* (Amphinomidae) (modified from Hartman 1951: fig. 1).—*3.* Lateral view of *Arenicola loveni* (Arenicolidae) (modified from Ashworth 1912: pl. 3, fig. 9).—*4.* Dorsal view of *Tharyx monilaris* (Cirratulidae) (Hartman 1960: pl. 12, fig. 2).—*5.* Lateral view of *Rhaphidrilus nemasoma* (Ctenodrilidae) (modified from Monticelli 1910: fig. 11).
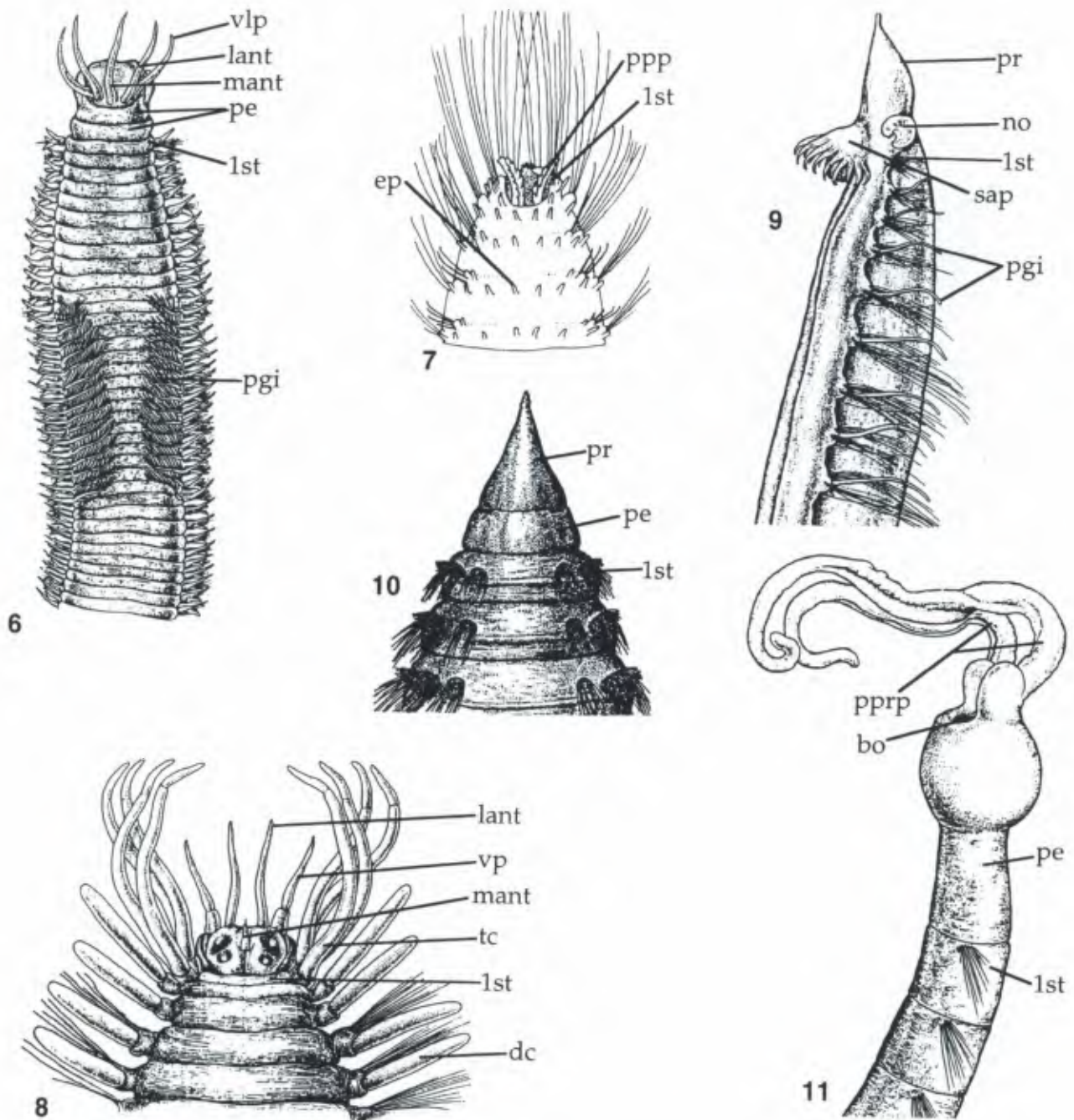
Figs 6–11. Polychaete anterior ends.—*6.* Dorsal view of *Marphysa disjuncta* (Eunicidae) (modified from Hartman 1961: pl. 10: fig. 1).—*7.* Dorsal view of *Piromis arenosus* (Flabelligeridae) (modified from Day 1967: fig. 32.4b).—*8.* Dorsal view of *Amphiduros pacifica* (Hesionidae) (modified from Hartman 1961: pl. 4, fig. 1).—*9.* Lateral view of *Ammotrypane pallida* (Opheliidae) (modified from Hartman 1960: pl. 14, fig. 3).—*10.* Dorsal view of *Orbinia johnsoni* (Orbiniidae) (modified from Hartman 1957: p. 21, fig. 3).—*11.* Lateral view of *Myriowenia californiensis* (Oweniidae) (modified from Hartman 1960: pl. 16, fig. 5).

authors (Pleijel 1995; Wilkinson 1995), but no real solutions have yet been posited. For example, the use of a character 'Palps' with two states, *absent* or *present*, does not currently allow for further characters based on the nature of the palps to be used in the same analysis. If further characters based on types of palps are added, then a '?' is usually added to the matrix for taxa for which the character is inappropriate. This applies to both binary and multistate forms of coding. However, taxa so scored will be assigned a state for the type of palps that may be meaningless (Platnick *et al.* 1991; Maddison 1993). The solution ultimately lies in new algorithms that will deal with hierarchical character linkage (Maddison 1993). In the meantime, this problem, when (or if) it is recognised by workers, can be addressed by using a FIG/FOG approach with a series of analyses at different hierarchical levels (Watrous & Wheeler 1981). Alternatively, the use of multistate characters has been advocated by Maddison (1993) and Meier (1994). This results in loss of information, as outlined by Pleijel (1995), such that a feature at a general level may be absent or present, but also exhibits some informative variation at a less general level. Hence, a multistate character will sacrifice the information at the more general

hierarchical level for the more restricted level. Absence/presence coding (A/P coding) is thought to have some advantages in that all features that can be discerned are coded as absent or present (Pleijel 1995). Meier (1994) argued for multistate coding and rejected A/P coding, but his points have been effectively refuted by Pleijel (1995). The logical application of A/P coding does, however, result in weighting of features that can be broken into many discrete characters. Pleijel (1995) suggested that perhaps this weighting can be alleviated by making the general character and all its subsidiaries have a total a priori weight that sums to 1. However, this presents problems when subsidiary characters are linked to more than one general character, or when a general character has several types of subsidiary characters. For example, the hypertrophied axial pharynges found in various polychaetes may have jaws of several kinds. Some also have a structure known as a proventricle that is arguably independent of the presence of jaws (Glasby 1993) but is dependent on the presence of a hypertrophied axial pharynx. Thus, there are two characters that are 'independently' linked to the presence of a hypertrophied axial pharynx. Weighing these characters *a priori* such that their sum weight
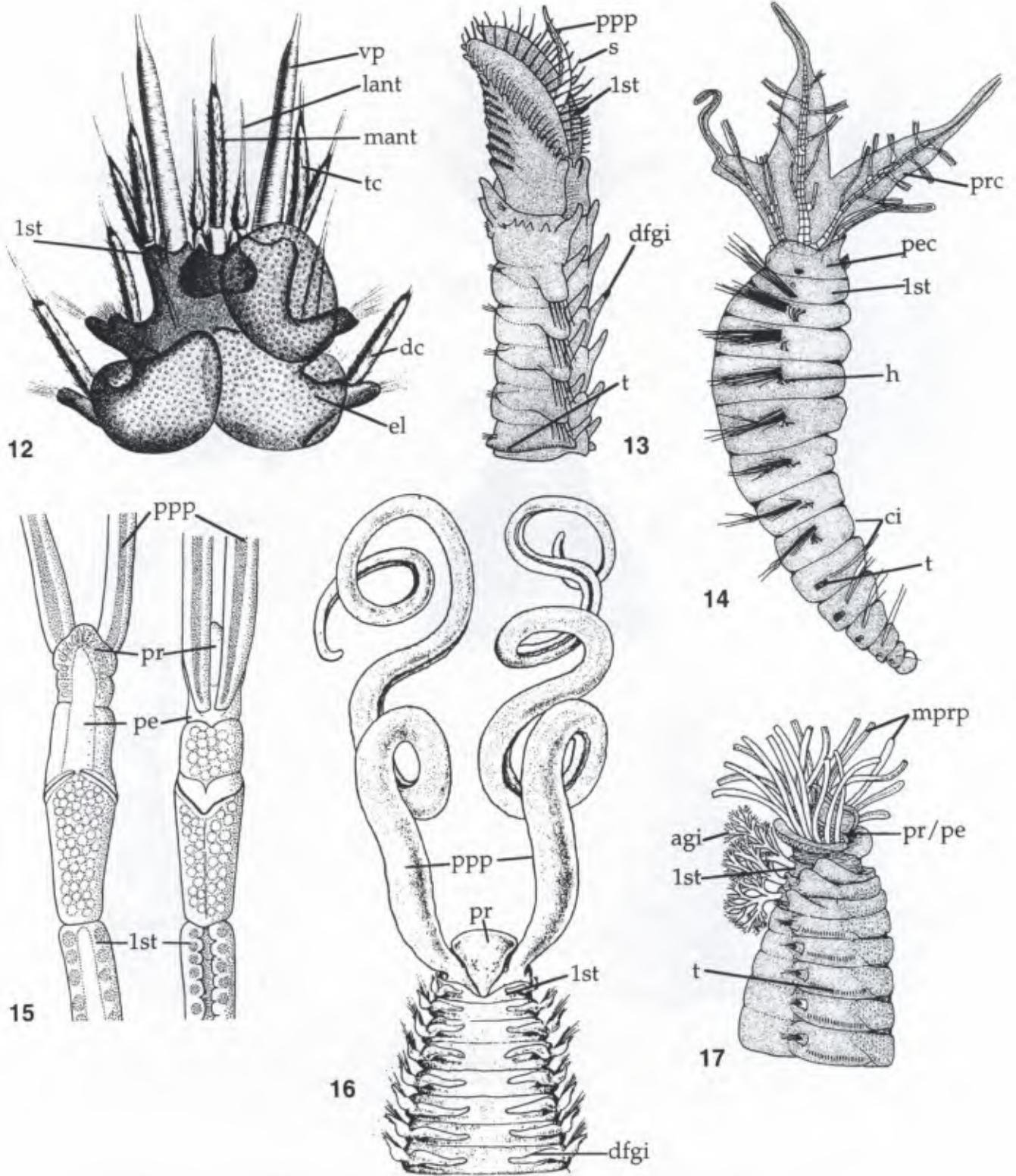
Figs 12–17. *Polychaete anterior ends.—12.* Dorsal view of *Harmothoe extenuata* (modified from Claparède 1868: pl. 2, fig. 2).—*13.* Lateral view of *Lygdamis indicus* (Sabellariidae) (modified from Day 1967: fig. 33.3c).—*14.* Lateral view of *Amphicorina androgyne* (Sabellidae) (modified from Rouse 1994: fig. 25).—*15.* Dorsal and ventral views of *Siboglinoides dibrachia* (Siboglinidae) (modified from Ivanov 1963: fig. Y133B, C).—*16.* Dorsal view of *Spio punctata* (Spionidae) (modified from Hartman 1961: pl. 11, fig. 1).—*17.* Lateral view of *Eupolymnia nebulosa* (Terebellidae) (modified from Day 1967: fig. 36.9h).

totals to one is artifactual since the more states that can be discerned within a feature, the lower the weight of each character.

Any a priori weighting scheme is going to be flawed since it does not really correct the problem. An attempt to control for linkage is applied here that treats the more general level of an arguably independent character with a value of 1. Any character that is clearly subsidiary to that character is given a value of 0.5, and any character that is in turn subsidiary is given a value of 0.25. Hence, 'Hypertrophied axial pharynges

A/P' is given a weight of 1; 'Hypertrophied axial pharynx with a proventricle A/P' is given a value of 0.5; 'Hypertrophied axial pharynges with jaws A/P' is also given a value of 0.5; 'Hypertrophied axial pharynx jaws as a lateral pair A/P' is given a weight of 0.25. This admittedly is arbitrary and is included as an acknowledgment of a problem rather than a solution. What should happen is that less general characters should not even be considered by the programs until those at a more general level have been utilised.
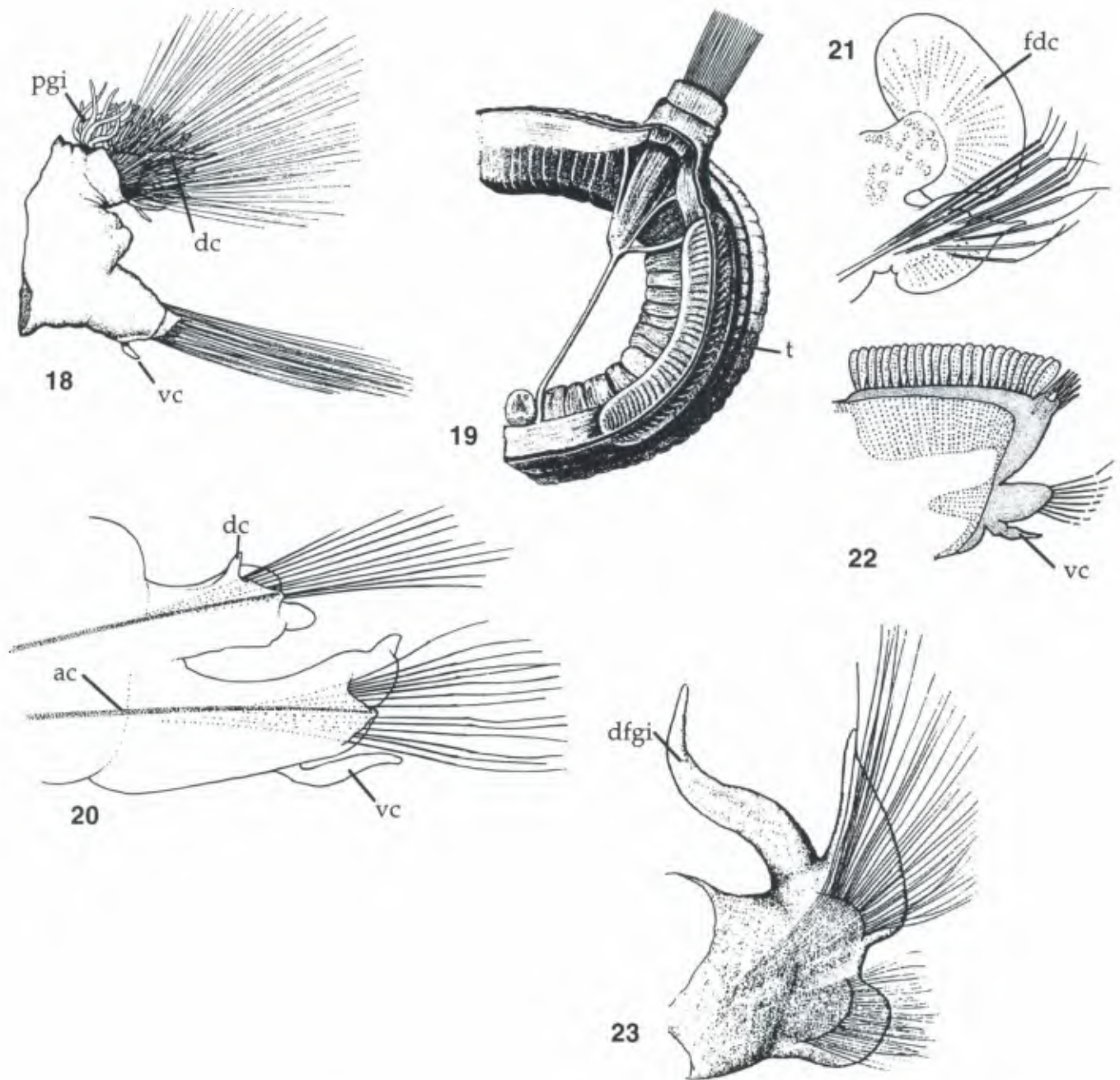
Figs 18–23. Polychaete parapodia.—*18*. Parapodium of *Pareurythoe americana* (Amphinomidae) showing similar rami (modified from Hartman 1951: pl. 7, fig. 1).—*19*. Transverse section of *Arenicola marina* (Arenicolidae) showing parapodium with torus of hooks (modified from Ashworth 1912: pl. 12, fig. 39).—*20*. Parapodium of *Paralacydonia paradoxa* (Paralacydoniidae) showing neuropodium larger than notopodium (modified from Hartman 1968: 329, fig. 2).—*21*. Parapodium of *Phyllodoce longipes* in (Phyllodocidae) showing foliaceous dorsal cirrus (modified from Hartman 1968: 229, fig. 3).—*22*. Parapodium of *Bhawania goodei* (Chrysopetalidae) showing notopodia across dorsum (modified from Day 1967: fig. 2.1c).—*23*. Spioniform parapodium of *Spio punctata* (Spionidae) showing dorsal flattened gill (modified from Hartman 1961: pl. 11, fig. 2).

The matrix based on A/P coding can be found in Appendix II. This matrix was used in analyses with all characters given equal weighting (*A/Pe*) and with weighting to control for hierarchical linkage (*A/Pw*). The weights assigned to the characters for the *A/Pw* analyses can be found in Appendix III. A matrix based on multistate coding that is derived from the A/P coding matrix is also used (Appendix II). The data matrices are available via the World Wide Web (WWW) from the following addresses: http://www.wallace.bio.usyd.edu.au/papers/gregr/. The multistate data matrix also includes the numerous apomorphic states that would be uninformative in the A/P coding analyses. In the case of the restricted analyses for both types of A/P coding, there are also uninformative characters or states present in restricted analyses that are informative when all taxa are included. All of the states found in multistate coding are outlined for the various taxa in Appendix I and discussed in Appendix IV. As pointed out by Pleijel (1995), multistate coding is flawed in that while homology hypotheses based on A/P coding are directly tested, no such test is made when one constructs a multistate character. Multistate coding also suffers from a lack of information retrievability, and there are distinct problems with inappropriate characters. However, since A/P coding is also flawed, a range of coding options is preferable at this time. With regards to inappropriate characters, the usual procedure of scoring them as unknown ('?') is used, with the attendant problems outlined by Platnick *et al.* (1991) and Maddison (1993).

Analyses are presented for the following:

1. *A/P* coding with equal weighting for both restricted and complete sets of taxa (= *A/Per*; *A/Pec*).

2. *A/P* coding with a priori weighting to control character linkage for both a restricted and complete sets of taxa (= *A/Pwr*; *A/Pwc*).

3. *Multistate* coding for both a complete and restricted set of taxa (*Mr*; *Mc*).

Analysis

Cladistic analyses were performed using PAUP 3.1.1 (Swofford 1993). Multistate characters were treated as unordered (non-additive), with initial equal weights, and unknown character states were coded as a '?'.
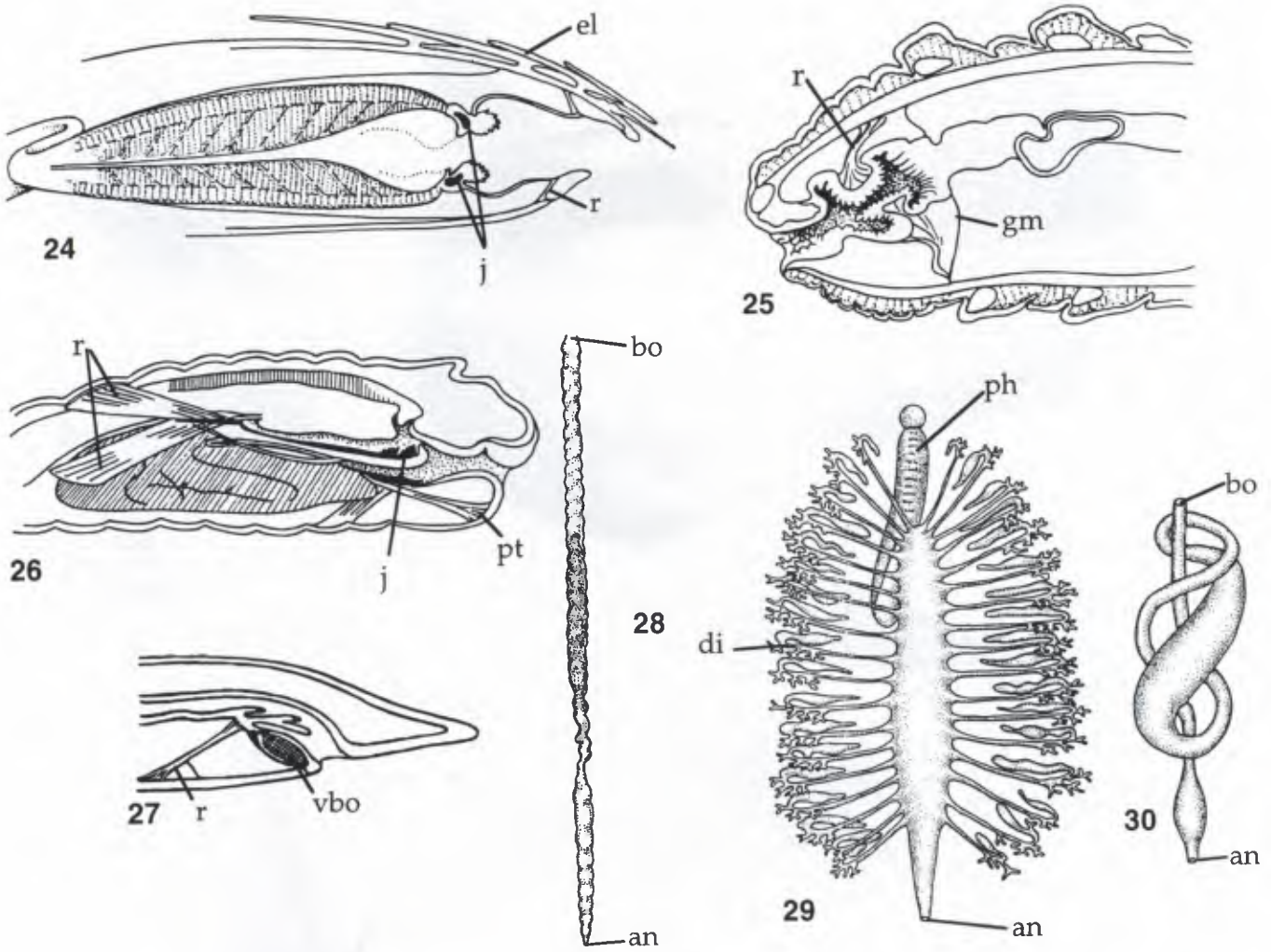
Figs 24–30. Polychaete pharynx and gut organization.—*24.* Drawing of sagittal section through *Aphrodite aculeata* (Polynoidae) showing hypertrophied axial pharynx (modified from Dales 1962: fig. 7A).—25. Drawing of sagittal section though anterior end of *Abarenicola vagabunda* (Arenicolidae) showing simple axial pharynx and gular membrane (modified from Dales 1962: fig. 13B).—26. Drawing of sagittal section though anterior end of *Marphysa sanguinea* (Eunicidae) showing hypertrophied ventral pharynx (modified from Dales 1962: fig. 9B).—27. Drawing of sagittal section though anterior end of generalised orbiniid showing eversible ventral buccal organ (modified from Dales 1963: fig. 5B).—28. Straight gut of *Owenia fusiformis* (modified from Brusca & Brusca 1990: 406, fig. 18B).—29. Gut with lateral diverticulae of *Aphrodita* sp. (Aphroditidae) (modified from Brusca & Brusca 1990: 409, fig. 18D).—30. Looped and folded gut of *Petta* sp. (Pectinariidae) (modified from Brusca & Brusca 1990: 409, fig. 18D).

For some taxa in multistate coding, the OR separator '/' was used since they obviously did not have some of the possible states in the character, and certain possibilities could be eliminated. Tree searches were performed using the heuristic search command and TBR. Between 50 and 100 random addition replicates were made for all analyses in order to locate possible 'islands' of trees (Maddison 1991). Zero-length branches were collapsed, and MULPARS was activated. The Sipuncula is used to root the most-parsimonious trees and polarise the transformations (Maddison *et al.* 1984; Nixon & Carpenter 1993). Ingroup taxa are outlined above. Characters, weights (*a priori*) and the data matrices are presented in Appendix I, Appendix II, Appendix III and Appendix IV. All analyses were subject to successive approximations character weighting (SW) (Farris 1969; Carpenter 1988), though this resulted in some cases in different trees than the original most-parsimonious trees. The values used to reweight the characters were based on the maximum values of the rescaled consistency indices and on a weight scale of 0–1000.

The trees derived from SW in the restricted analyses were then assessed for 'branch support' (*b*) (Bremer 1988,1994), also known as the 'decay index', 'support index' or 'Bremer support' (Donoghue *et al.* 1992; Källersjö *et al.* 1992; Davis 1993). This was calculated using the program AutoDecay 2.9.5 (Eriksson 1996) in association with PAUP 3.1.1. Ten random addition searches were conducted for each of the constraint trees generated by AutoDecay, except for the *Mr* analysis where the 'closest' option was used to save computing time. To make the trees derived from SW comparable in terms of the initial weight values of the matrices, the weighted extra length of the trees was rescaled by dividing the weighted length of the most-parsimonious trees (*sw*) by the length of the initial

most-parsimonious trees (*s*). This factor was then used to provide the weighted rescaled branch support (*bwr*) values (Bremer 1994; Gustaffson & Bremer 1995). The total support (*t*) and total support index (*ti*) for the trees derived from SW in restricted analyses were also calculated.

Character transformations were studied using MacClade 3.06

Analysis of character state distributions and optimisations were performed using PAUP and MacClade 3.01 (Maddison & Maddison 1996). MacClade assesses all possible transformations, including both 'delayed' transformations and 'accelerated' transformations, though, for this study, unambiguous transformations were mainly considered, owing to the number of characters and trees involved. Analysis of association of characters using Fischer's exact probability test was made using Statistica 1.5 (StatSoft Inc.).

Abbreviations used in figures

1st	first segment
agi	anterior gills
an	anus
bo	buccal opening
bv	blood vessel
ca	caruncle
cc	closed circulatory system
ci	chaetal inversion
cj	cross of jaws
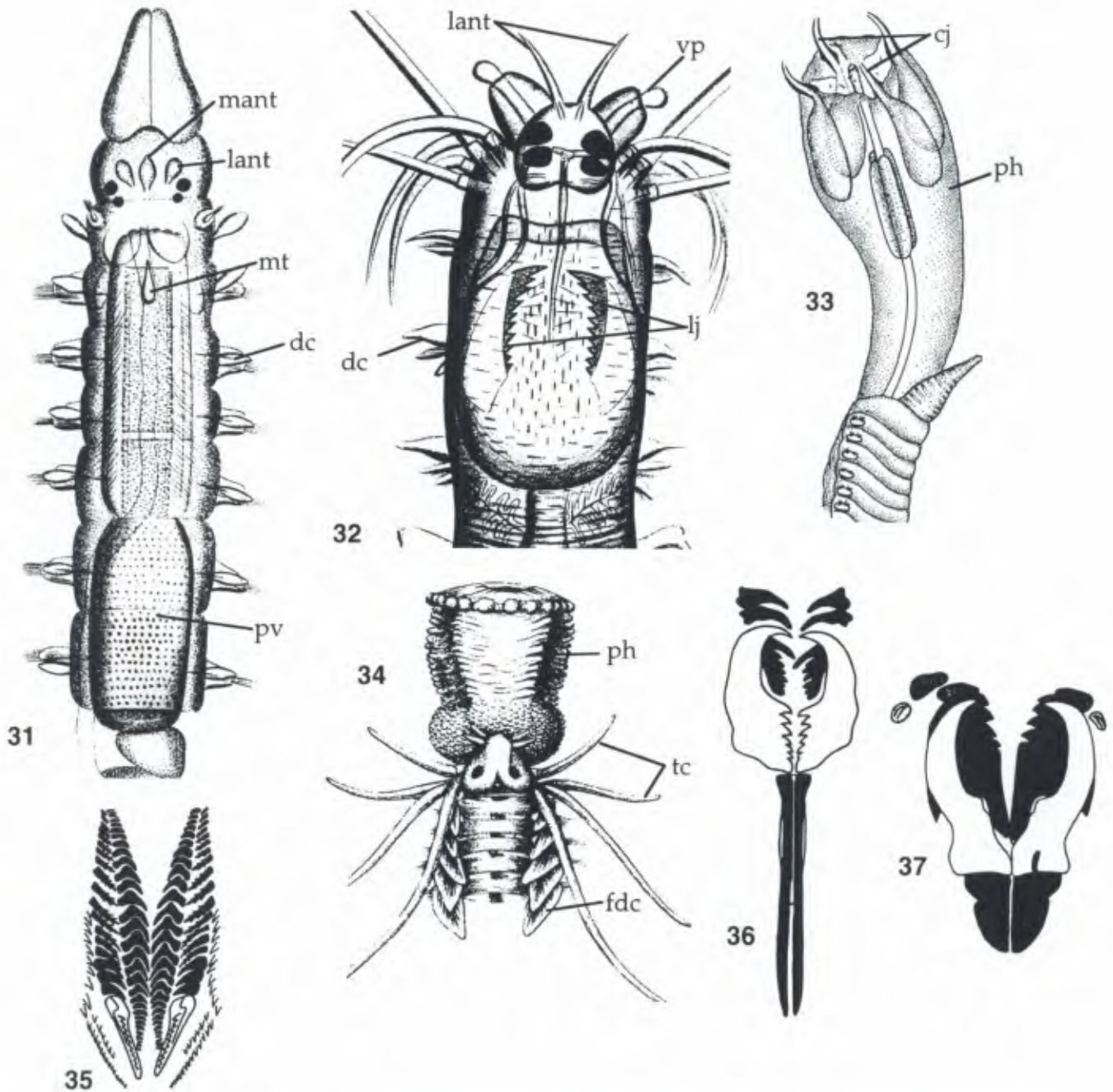
Figs 31–37. Polychaete pharynges and jaws.—*31.* Dorsal view of anterior end of *Exogone veruger* (Syllidae) showing proventricle and median tooth (modified from Claparède 1868: pl. 12, fig. 3).—*32.* Dorsal view of *Nereis dumerilii* (Nereididae) showing pair of lateral jaws (modified from Claparède 1870: pl. 4, fig. 1).—*33.* Lateral view of *Glycera convoluta* (Glyceridae) with hypertrophied axial pharynx everted showing two pairs of jaws forming a cross (modified from Brusca & Brusca 1990: 400, fig. 14).—*34.* Dorsal view of *Phyllodoce lamelligera* (Phyllodocidae) showing jawless pharynx (McIntosh 1908: pl. 63, fig. 20).—*35.* Ctenognath jaws of a dorvilleid (modified from Kielan-Jaworowska 1966: fig. 5E).—*36.* Prionognath jaws of Oenonidae (modified from Kielan-Jaworowska 1966: fig. 5M).—*37.* Labidognath jaws of Eunicidae (modified from Kielan-Jaworowska 1966: fig. 5H).

co	coelomostome/coelomoduct	*mne*	metanephridium
dc	dorsal cirri	*mpp*	multiple peristomial palps
dgi	dorsal simple gills	*mprp*	multiple prostomial palps
dfgi	dorsal flattened gills	*mt*	median tooth
di	gut diverticula	*ned*	nephridioduct
el	elytra	*no*	nuchal organ
ep	epidermal papillae	*pe*	peristomium
fdc	foliaceous dorsal cirrus	*pec*	peristomial ring and collar
g	gametes	*pgi*	parapodial gills
gm	gular membrane	*ph*	pharynx
h	hook	*pne*	protonephridium
hb	heart body	*ppp*	paired peristomial grooved palps
j	jaws	*pprp*	paired prostomial grooved palps
lant	lateral antennae	*pr*	prostomium
lj	lateral jaws	*pe*	peristomium
mant	median antenna	*pr/pe*	prostomium fused with peristomium
mix	mixonephridium	*prc*	prostomial crown
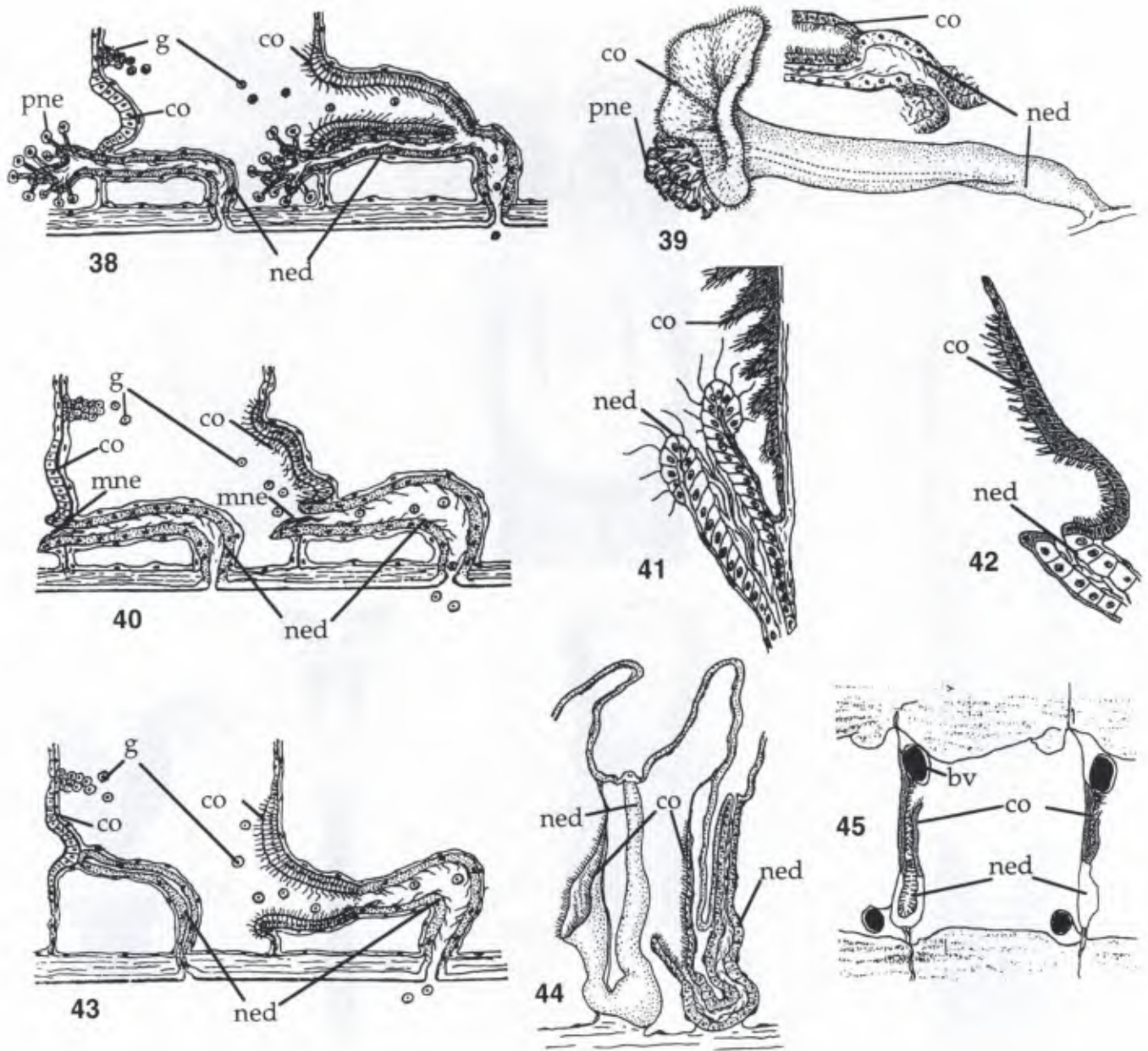
Figs 38–45. Polychaete segmental organs.—38. Development of protonephromixia. Early stage (left) with protonephridium formed and coelomoduct beginning. Mature stage (right) with coelomoduct fused with nephridioduct (modified from Goodrich 1945: fig. 1). Note arguments by Bartolomaeus (1989) reject this interpretation (see text).—39. Protonephromixium of *Nereiphylla paretti* (Phyllodocidae) showing mesodermal coelomoduct fused with protonephridium and histological section though point of fusion (modified from Goodrich 1945: figs 24a, b). Work by Bartolomaeus (1989) would suggest that this should be interpreted as ectodermal protonephridium and metanephridium co-existing with no mesodermal component (see text).—40. Development of metanephromixia. Early stage (left) with metanephridium formed and coelomoduct beginning. Mature stage (right) with coelomoduct fused with nephridioduct (modified from Goodrich 1945: fig. 2).—41. Longitudinal section of a mature metanephromixium of *Hesione sicula* (Hesionidae) showing coelomostome and metanephridium with clear nephrostome (modified from Goodrich 1945: fig. 39b).—42. Longitudinal section of another mature metanephromixium of *Ophiodromus flexuosus* (Hesionidae) showing a closer association of the coelomostome with the metanephridium and nephrostome reduced or absent (modified from Goodrich 1945: fig. 39c).—43. Development of mixonephridium. Early stage (left) with metanephridium and coelomostome forming. Mature stage (right) with coelomostome fused with nephridioduct (modified from Goodrich 1945: fig. 3).—44. Drawing of whole (left) and longitudinal section (right) through segmental organs of *Nerines* sp. (Spionidae) apparently showing coelomostome grafted onto nephridioduct (modified from Goodrich 1945: fig. 45). Goodrich (1945) was equivocal about the classification of the segmental organs of this group but results shown here suggest they should be classified as mixonephridia.—45. Drawing of longitudinal section through segments of *Marphysa sanguinea* (Eunicidae) showing coelomostomes fused with nephridioducts (modified from Goodrich 1900: fig. 21).

pt	protractor
pv	proventricle
r	retractor
sap	simple axial pharynx
s	spine
t	torus of hooks or uncini
tc	tentacular cirrus
vbo	ventral buccal organ
vlp	ventro-lateral palps
vp	ventral palps

Results

Restricted analyses

A/Per analysis. With 29 families deleted, 330 most-parsimonious trees with lengths of 346 steps were found, each with a consistency index (ci) of 0.355 and a retention index (ri) of 0.763. The strict consensus of these 330 trees is
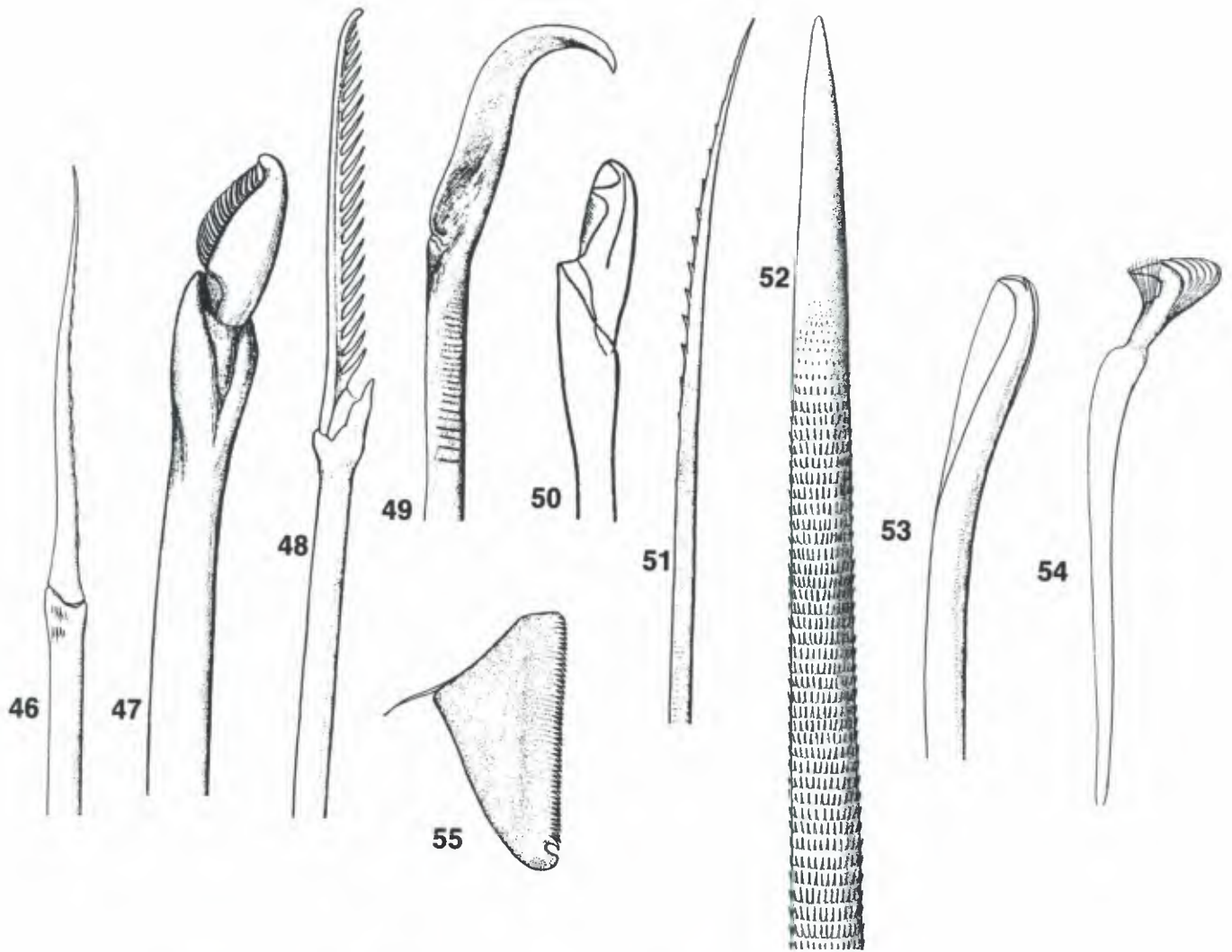
Figs 46–55. *Palychaete chaetae.—46.* Tapering compound chaeta with single ligament of *Leanira calcis* (Sigalionidae) (modified from Hartman 1960: pl. 4, fig. 2).—*47.* Falcate compound chaeta with single ligament of *Ceratocephale edmondsi* (Nereididae) (modified from Hartman 1954b: fig. 16).—*48.* Dentate compound chaeta with single ligament of *Exogonella brunnea* (Syllidae) (modified from Hartman 1961: pl. 8, fig. 4).—*49.* Hooked compound chaeta with fold of *Flabelliderma essenbergae* (Flabelligeridae) (modified from Hartman 1968: 288, fig. 5).—*50.* Dentate compound chaeta with double ligament of *Eunice longicirrata* (Eunicidae) (modified from Hartman 1944a: pl. 6, fig. 122).—*51.* Capillary chaeta of *Oxydromus brunnea* (Hesionidae) (modified from Hartman 1961: pl. 5, fig. 3).—*52.* Spine of *Lagisca pedroensis* (Polynoidae) (modified from Hartman 1960: pl. 3, fig. 5).—*53.* Hooded chaeta of *Spio punctata* (Spionidae) (modified from Hartman 1961: pl. 11, fig. 3).—*54.* Hook of *Praxillella trifila* (Maldanidae) (modified from Hartman 1960: pl. 15, fig. 4).—*55.* Uncinus of *Phyllochaetopterus limicolus* (Chaetopteridae) (modified from Hartman 1960: pl. 10, fig. 5).

shown in Fig. 56. After SW, two trees of weighted length 101 261 ($ci = 0.616$; $ri = 0.894$) were found that were both different (not congruent) in topology to those originally found and corresponded to an original weighted length of 348 steps. The strict consensus of these two trees is shown in Fig. 57. The major difference between the SW derived trees and the original trees is the much greater resolution of relationships and the shift of the clade (Arenicolidae, Capitellidae, Maldanidae) to a more basal position.

The weighted branch support values (*bwr*) for trees derived from SW are show next to the nodes of the consensus tree on Fig. 57. The values have been rescaled to be more directly comparable to the original weighting that gave the initial trees. The total support (*t*) value for the tree is 189.6, giving a total support index (*ti*) of 0.77.

A/Pwr analysis. Nine most-parsimonious trees were found with lengths of 236.125 ($ci = 0.347$; $ri = 0.753$). The strict consensus of these 9 trees is shown in Fig. 58. After SW, three shortest trees were found of length 90 910 ($ci = 0.638$;

$ri = 0.898$) that were different (not congruent) in topology to those originally found and corresponded to an initial weighted length of 237.375. The strict consensus of these trees is shown in Fig. 59. The major difference between the SW derived trees and the original trees is the shift of clade (Arenicolidae, Capitellidae, Maldanidae) to a more basal position. The weighted branch support values (*bwr*) for trees derived from SW are shown next to the nodes of the consensus tree on Fig. 59. They have been rescaled to be more directly comparable to the original weights that gave the initial shortest trees. The total support (*t*) value for the tree shown in Fig. 59 is 133.7, and the total support index (*ti*) is 0.56.

Mr analysis. With 29 families deleted, 1308 most-parsimonious trees with lengths of 241 steps ($ci = 0.523$; $ri = 0.796$) were found. The strict consensus of these trees is shown in Fig. 60. After SW, 431 shortest trees were found with a weighted length of 95 421 ($ci = 0.679$; $ri = 0.888$) that were slightly different in topology to those originally found

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57
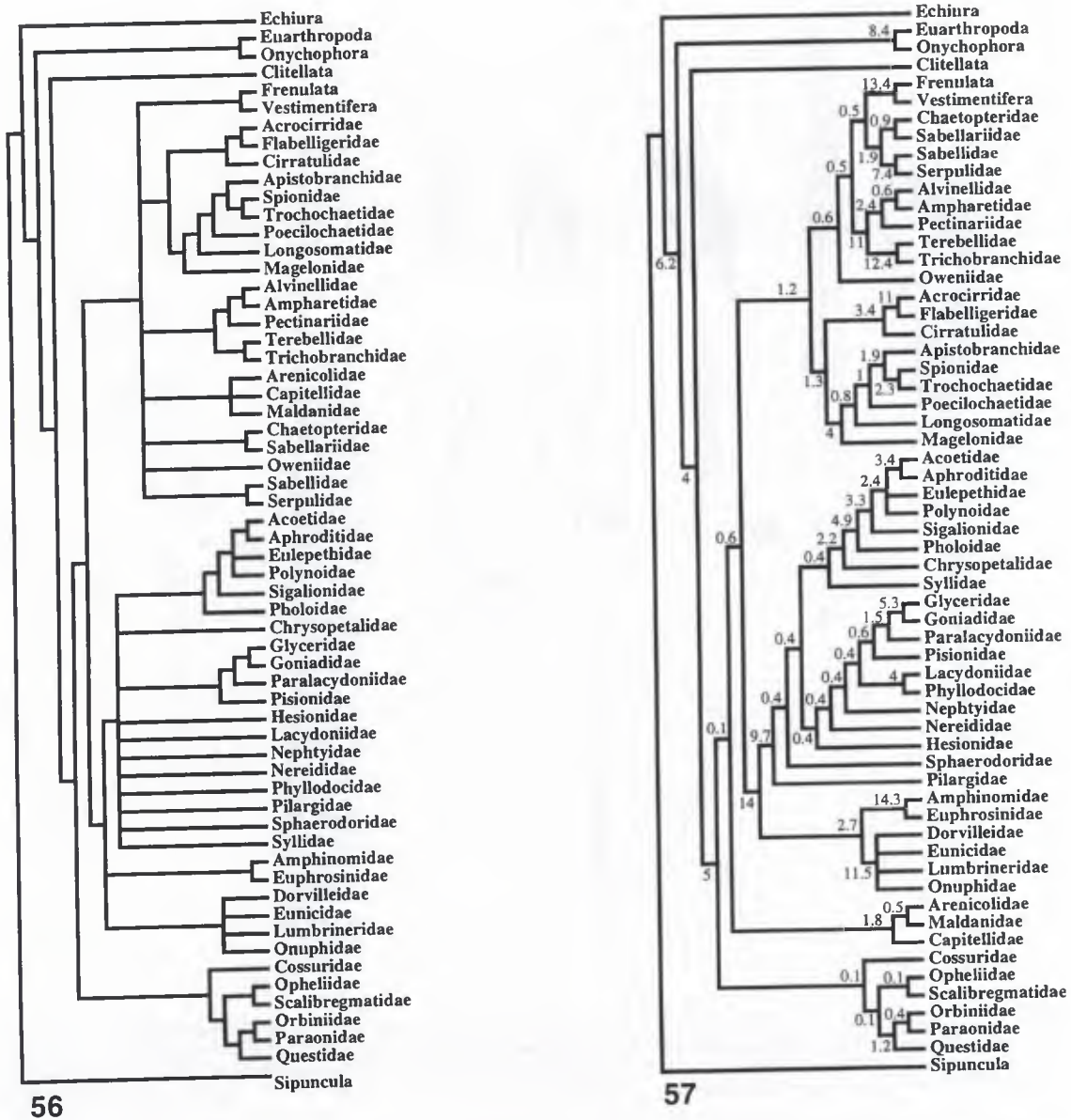
Figs 56–57. Consensus trees based on the *A/Per* analysis.—*56.* Strict consensus trees of 330 initial most-parsimonious trees (length 346).—*57.* Strict consensus trees of two most-parsimonious trees found after SW (equivalent to initial weighted length of 348). Values below each node indicate rescaled branch support (*b*) values (rounded to one decimal point).

and were one step longer at 242 steps. The strict consensus of these trees is shown in Fig. 61. The major difference between the initial trees and the SW trees is that the clade of six families Cossuridae, Opheliidae, Orbiniidae, Paraonidae, Questidae and Scalibregmatidae in the former analysis becomes a grade in the SW trees.

The weighted branch support values (*bwr*) for the trees derived from SW are shown next to the nodes on Fig. 61. They have been rescaled to be more directly comparable to the weights that gave the original trees. The total support (*t*) value for the tree shown in Fig. 61 is 189.7, and the total support index (*ti*) is 0.78.

Complete analyses

A/Pec analysis. With all taxa included, 6907 most-parsimonious trees with lengths of 513 steps were found (ci = 0.242; ri = 0.721). The strict consensus of these trees is shown in Fig. 62. After several iterations of SW, 25 trees of

length 86 716 (ci = 0.479; ri = 0.842) were found that were different in topology to those originally found and corresponded to an original weighted length of 517 steps. The strict consensus of these two trees is shown in Fig. 63.

A/Pwc analysis. There were 468 most-parsimonious trees found in an analysis of all taxa with a length of 354.5 (ci = 0.232; ri = 0.713). The strict consensus of these shortest trees is shown in Fig. 64. After SW, eight shortest trees were found with length 77 595 (ci = 0.476; ri = 0.854) that were different in topology to those originally found and corresponded to an original weighted length of 359.375. The strict consensus of these trees is shown in Fig. 65. There are major differences between the SW derived trees and the original trees. For example, Fig. 65 shows a clade (Aeolosomatidae Potamodrilidae Parergodrilidae) as plesiomorphic, whereas in the original trees, these taxa are quite derived.

Mc analysis. With all taxa included, more than 19 000
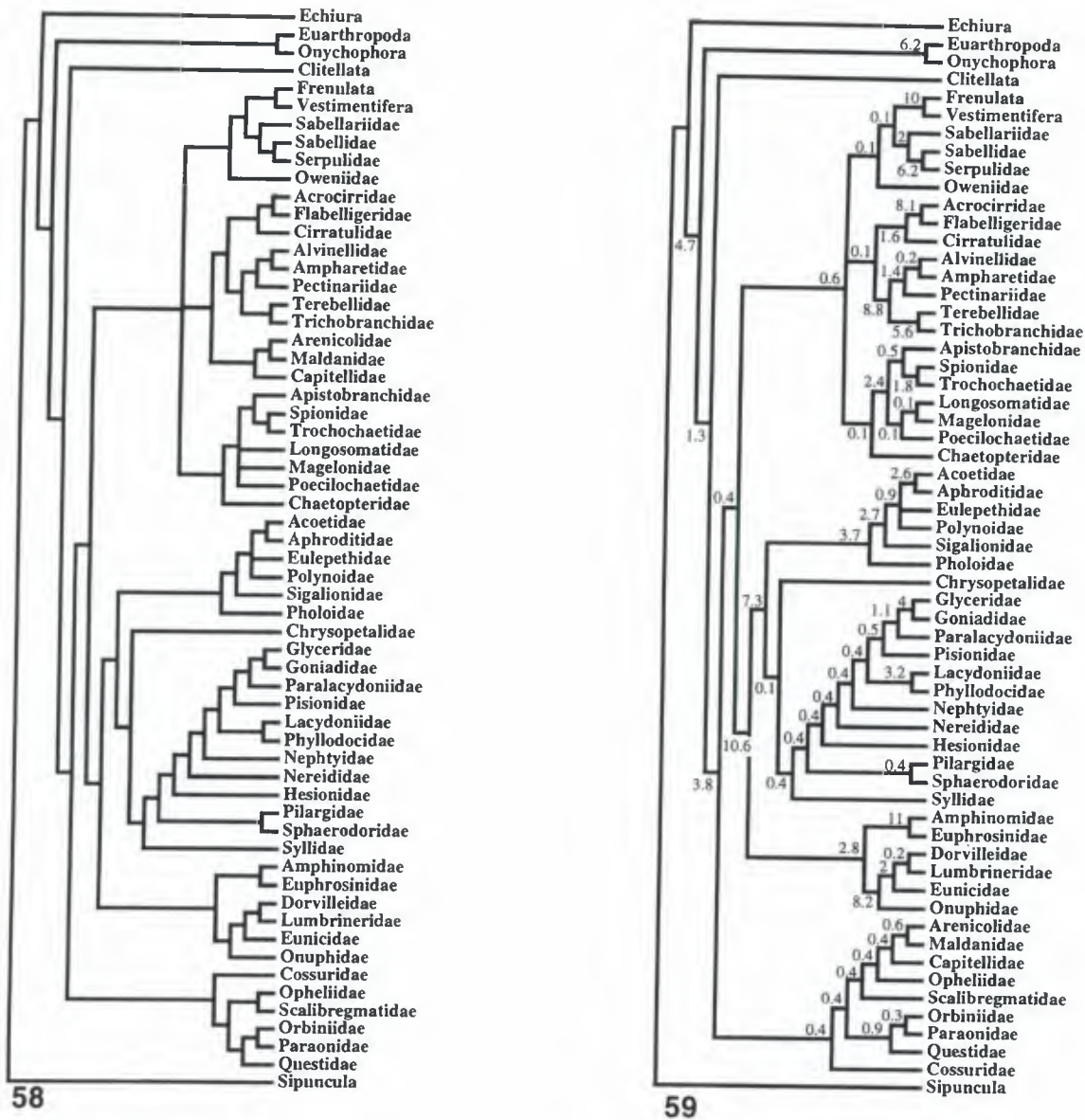
Figs 58–59. Consensus trees based on the *A/Pwr* analysis.—*58.* Strict consensus trees of nine initial most-parsimonious trees (length 236.125).—*59.* Strict consensus of three most-parsimonious trees found after SW (equivalent to initial weighted length of 237.375). Values below each node indicate rescaled branch support (*b*) values (rounded to one decimal point).

most-parsimonious trees with lengths of 337 steps were found (ci = 0.395; ri = 0. 755) before the computer memory was exhausted. Many more trees of this length were possible and not found, and shorter trees may exist. The strict consensus of the 19 300 trees found before memory overflowed is shown in Fig. 66. Successive weighting was not performed in this analysis because all most-parsimonious trees were not obtained.

Descriptions of trees and transformations

Restricted analyses. All descriptions of transformations are with reference to trees derived from SW. The taxon Articulata formulated by Rouse & Fauchald (1995) contained a polytomy that is now resolved. In all three coding methods, the Arthropoda are a sister group to a monophyletic Annelida (formulated below). In the *A/Pwr* analysis, the Articulata is supported by the presence of segmentation and longitudinal muscles divided into bands

and also the presence of a straight gut (Fig. 67). In the *Mr* analysis, the Articulata is supported by the presence of segmentation and longitudinal muscles divided into bands (Fig. 71). These are the same two features that supported the Articulata in Rouse & Fauchald (1995). The Echiura is the sister group to the Articulata in all trees with all coding methods. The presence of chaetae has alternative transformations in all trees such that they appear in the Echiura and Annelida independently or they have been lost in the Arthropoda. In *Mr* trees, based on unambiguous transformations, the Echiura is the sister group to the Articulata based on a peristomium limited to lips (m 2) and the presence of a closed circulatory system (m 41) (Fig. 71). In all *A/Per* and *A/Pwr* trees, the loss of the limited (or absent) circulatory system is the only unambiguous character state supporting the clade (Echiura Articulata) (e.g. Fig. 67).

All three coding methods found a monophyletic Annelida with the Clitellata as sister group to a Polychaeta that includes the Pogonophora.
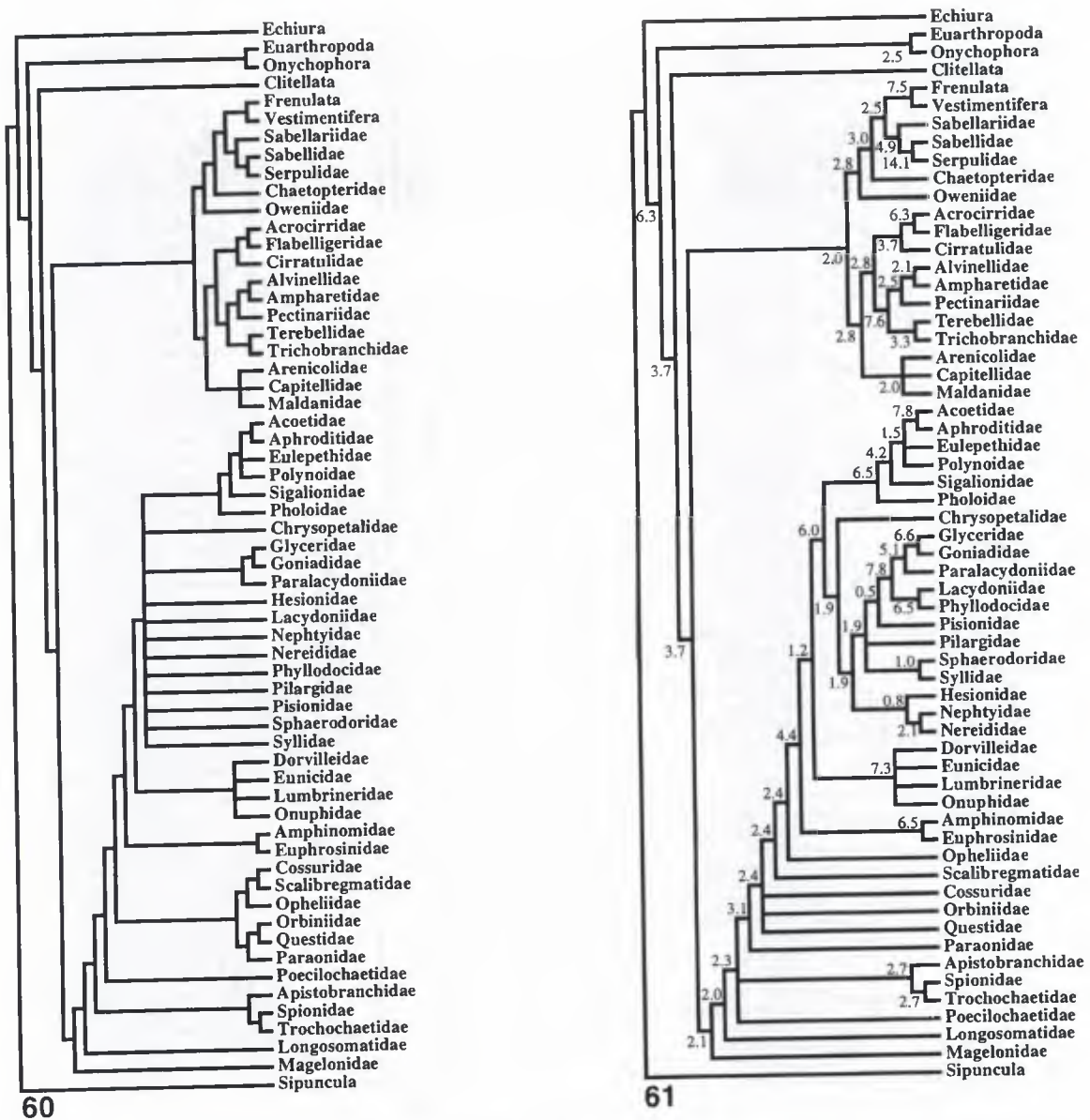
Figs 60–61. Consensus trees based on the *Mr* analysis.—*60*. Strict consensus trees of 1308 initial most-parsimonious trees (length 241).—*61*. Strict consensus of 431 most-parsimonious trees found after SW (equivalent to initial weighted length of 242). Values below each node indicate rescaled branch support (*b*) values (rounded to one decimal point).

In *Mr* trees, the monophyly of this Annelida is indicated by the state of having the first body segments similar to those following (m 14), dorso-lateral folds in the buccal cavity (m 26) and the presence of capillary chaetae (m 49) (Fig. 71). In *A/P* trees (both forms), the Annelida is supported by the same three features found in multistate coding, as well as having the prostomium separated from the peristomium by a distinct groove (A/P 1), and the first segment appendages the same as those following (A/P 37) (Fig. 67).

The monophyly of the Polychaeta (including the Pogonophora) is supported in *Mr* trees by the (homoplastic) presence of palps (m 5) and the presence of mixonephridia (m 37) (Fig. 72). In *A/Per* and *A/Pwr* trees, the Polychaeta is supported by the presence of nuchal organs (A/P 25), nuchal organs as pits or grooves (A/P 26), parapodia (A/P 44) and mixonephridia (A/P 92) (Fig. 67).

The description and discussion of the numerous transformation series involved in this study is simply too

much for a single paper, especially since the three coding methods often give different transformations. Rather than document and discuss all transformations, the unambiguous transformations have been outlined for the restricted taxa analyses for two of the coding methods, *A/Pwr* and *Mr*, though many of the transformations in the *A/Per* trees are the same as *A/Pwr* trees. Figure 67 shows the unambiguous changes in characters in the basal region of one of the three *A/Pwr* trees derived from SW. The Polychaeta is then represented in Figs 68–70, which show the major clades. Figures 71, 72 show the unambiguous transformations for one of the 431 SW trees obtained for *Mr* analysis.

In the restricted taxa analyses, there is agreement among the three coding methods for much of the cladistic pattern of the Polychaeta. All three methods result in strong support for a clade comprising all eunicemorph, 'amphinomid' and phyllodocemorph taxa, though the relationships amongst these taxa vary. Both *A/Per* and *A/Pwr* trees show a weakly supported clade identified by the presence

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Echiura
Euarthropoda
Onychophora
Clitellata
Frenulata
Vestimentifera
Acoetidae
Aphroditidae
Eulepethidae
Polynoidae
Sigalionidae
Pholoidae
Chrysopetalidae
Glyceridae
Goniadidae
Paralacydoniidae
Pisionidae
Lacydoniidae
Nephtyidae
Nereididae
Phyllodocidae
Pilargidae
Tomopteridae
Typhloscolecidae
Sphaerodoridae
Alciopidae
Iospilidae
Lopadorhynchidae
Pontodoridae
Hesionidae
Ichthyotomidae
Syllidae
Nautiliniellidae
Amphinomidae
Euphrosinidae
Dorvilleidae
Eunicidae
Onuphidae
Lumbrineridae
Oenonidae
Hartmaniellidae
Aberrantidae
Nerillidae
Paraonidae
Acrocirridae
Flabelligeridae
Fauveliopsidae
Pocobiidae
Cirratulidae
Ctenodrilidae
Alvinellidae
Ampharetidae
Pectinariidae
Terebellidae
Trichobranchidae
Apistobranchidae
Spionidae
Uncispionidae
Trochochaetidae
Longosomatidae
Magelonidae
Poecilochaetidae
Arenicolidae
Maldanidae
Capitellidae
Psammodrilidae
Chaetopteridae
Cossuridae
Opheliidae
Orbiniidae
Oweniidae
Polygordiidae
Protodrilidae
Protodriloididae
Saccocirridae
Questidae
Sabellariidae
Sabellidae
Serpulidae
Scalibregmatidae
Aeolosomatidae
Parergodrilidae
Potamodrilidae
Sternaspidae
Myzostomidae
Spintheridae
Diurodrilidae
Histriobdellidae
Sipuncula

63

Echiura
Euarthropoda
Onychophora
Clitellata
Frenulata
Vestimentifera
Alvinellidae
Ampharetidae
Pectinariidae
Terebellidae
Trichobranchidae
Chaetopteridae
Sabellariidae
Sabellidae
Serpulidae
Arenicolidae
Maldanidae
Capitellidae
Psammodrilidae
Acoetidae
Aphroditidae
Eulepethidae
Polynoidae
Sigalionidae
Pholoidae
Chrysopetalidae
Glyceridae
Goniadidae
Paralacydoniidae
Pisionidae
Lacydoniidae
Lopadorhynchidae
Phyllodocidae
Alciopidae
Typhloscolecidae
Sphaerodoridae
Tomopteridae
Pilargidae
Pontodoridae
Nephtyidae
Nereididae
Iospilidae
Hesionidae
Ichthyotomidae
Syllidae
Nautiliniellidae
Amphinomidae
Euphrosinidae
Dorvilleidae
Eunicidae
Onuphidae
Lumbrineridae
Oenonidae
Hartmaniellidae
Aberrantidae
Nerillidae
Acrocirridae
Flabelligeridae
Fauveliopsidae
Poeobiidae
Cirratulidae
Apistobranchidae
Spionidae
Uncispionidae
Trochochaetidae
Poecilochaetidae
Longosomatidae
Magelonidae
Oweniidae
Polygordiidae
Protodrilidae
Protodriloididae
Saccocirridae
Aeolosomatidae
Parergodrilidae
Potamodrilidae
Ctenodrilidae
Cossuridae
Opheliidae
Scalibregmatidae
Orbiniidae
Paraonidae
Questidae
Sternaspidae
Myzostomidae
Spintheridae
Diurodrilidae
Histriobdellidae
Sipuncula

Figs 62–63. Consensus trees based on the *A/Pec* analysis.—*62.* Strict consensus trees of 6907 initial most-parsimonious trees (length 513).—*63.* Strict consensus of 25 most-parsimonious trees found after SW (equivalent to initial weighted length of 517).

of grooved palps (*A/Pwr* result shown in Figs 59, 70). The trees from the *Mr* analysis differ from the *A/Per* and *A/Pwr* trees in this respect in that there is a grade of taxa with grooved palps (Figs 61, 71). The *A/Pwr* trees show a clade of polychaetes, comprising nine families, that is the sister group to the remaining polychaete taxa, though it is weakly supported (Figs 59, 68). In *A/Per* trees, this clade appears as a grade (Fig. 57), and in multistate coding, the Arenicolidae, Capitellidae and Maldanidae are the sister group to a clade with grooved palps, and the other taxa form a grade between the spiomorphs and the clade identified by, amongst other features, aciculae (Figs 61, 71).

In all coding methods, the clade (Frenulata Vestimentifera) appear as the sister group to a clade that minimally includes the Sabellidae, Serpulidae and Sabellariidae (Figs 56–66, 70, 71). The monophyly of the (Frenulata Vestimentifera) is strongly supported in all analyses, and it is clear that this group must now be considered as a clade of the Polychaeta. The unequivocal character state changes that support the clade ((Frenulata Vestimentifera) (Sabellariidae (Serpulidae Sabellidae))) in *A/Pwr* trees (Fig. 70) are the loss of dorso-lateral folds (A/P 66), the presence of a pair of anterior excretory nephridia and posterior gonoducts (A/P 97) and the presence of uncini (A/P 123). While the absence of dorso-lateral folds is obviously a

64

65
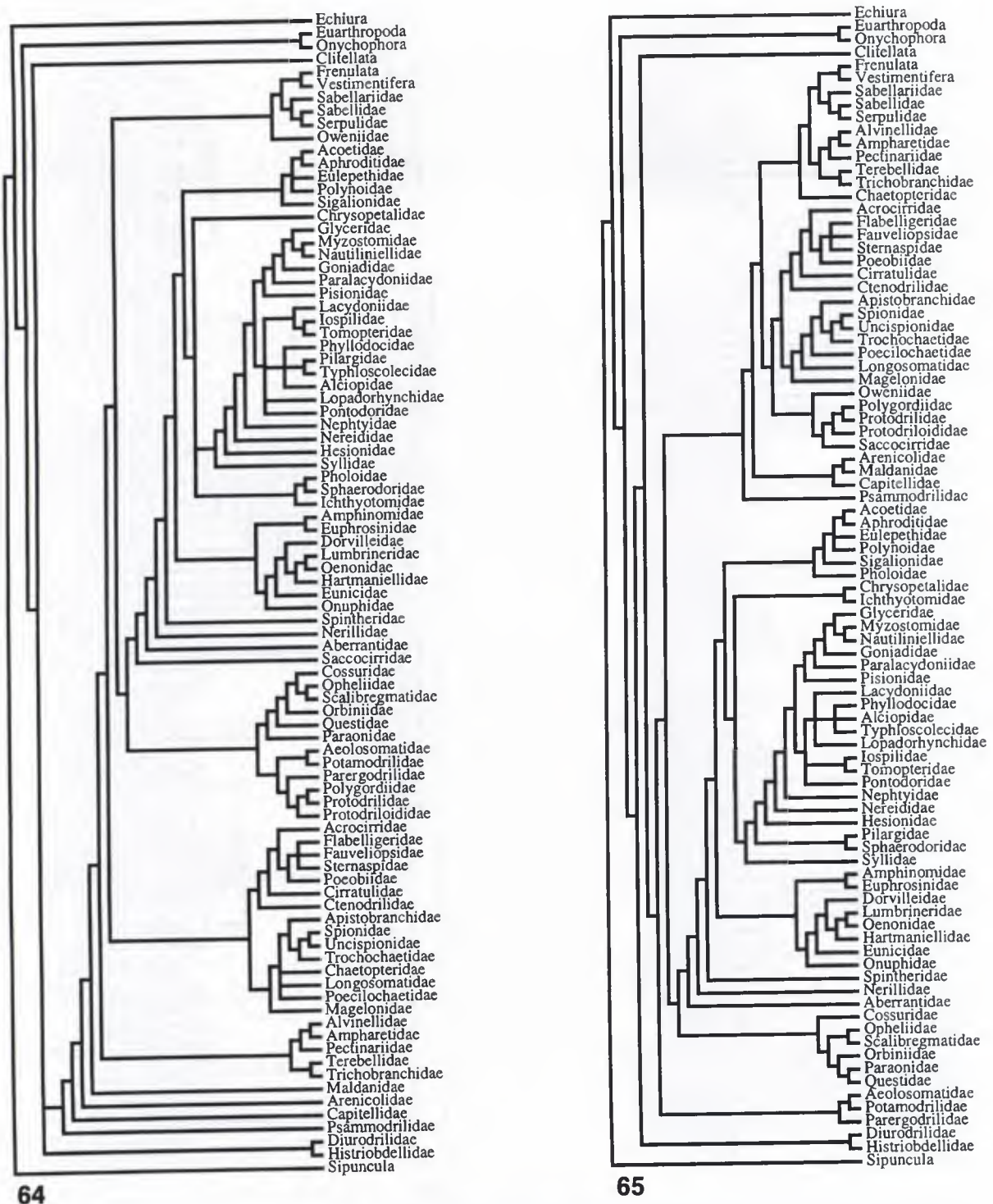
Figs 64–65. Consensus trees based on the *A/Pwc* analysis.—*64.* Strict consensus trees of 468 initial most-parsimonious trees (length 354.5).—*65.* Strict consensus of eight most-parsimonious trees found after SW (equivalent to initial weighted length of 359.375).

reversal since it is an apomorphic feature of the Annelida (Fig. 67), the latter two characters are also homoplastic, with the presence of a pair of anterior excretory nephridia supporting the ((Acrocirridae Flabelligeridae) Cirratulidae) clade and the presence of uncini also supporting a clade containing terebellids and associated taxa (Fig. 70). In *Mr* trees, the presence (also homoplastic) of an anterior pair of excretory nephridia (m 39) is the only unambiguous state supporting the ((Frenulata Vestimentifera) (Sabellariidae (Serpulidae Sabellidae))) (Fig. 71).

Complete analyses. For the results based on A/P coding, the descriptions of groupings are with reference to the trees

derived from SW, though the initial weighted trees are listed when they agree with the SW trees. For the *Mc* analysis, only the initial analysis is discussed since all most-parsimonious trees were not found, and therefore, SW was not performed. No detailed study of the transformations series found in the complete analyses is presented here. In the *A/Pec* and *A/Pwc* analyses, the taxa Diurodrilidae and Histriobdellidae are the sister group to a clade comprising the Clitellata and all taxa except for the Sipuncula, Echiura and arthropods (Figs 62–65). In the *Mc* analysis, the Echiura is sister group to all of the remaining ingroup taxa, and a traditionally formulated Annelida is not supported since the arthropod taxa are part of a polytomy with all the

Fig. 66. Consensus tree based on the *Mc* analysis. Strict consensus trees of 19 300 of the shortest trees (length 337) found before computer memory overflowed.

In all forms of complete analysis, the Aberrantidae appears as a basal member of a clade whose other members have a hypertrophied axial or ventral pharynx (Figs 62–66). The Nerillidae occupy a similar position in all three analyses (Figs 62–66). The Uncispionidae groups with spioniform taxa in all complete analyses (Figs 62–66). The two families that have a hypertrophied ventral pharynx and were excluded in the restricted analyses, the Oenonidae and Hartmaniellidae, form a clade with the other taxa having this feature in all the complete analyses (Figs 62–66).

The taxa Fauveliopsidae, Poeobiidae and Sternaspidae form a clade with the Acrocirridae, Cirratulidae and Flabelligeridae in both the *A/Pwc* and *Mc* analyses (Figs 65, 66). In the *A/Pec* analysis, the Fauveliopsidae and Poeobiidae also form a clade with the Acrocirridae, Cirratulidae and Flabelligeridae. However, in that analysis, the Sternaspidae belongs to a clade comprising the Cossuridae, Opheliidae, Orbiniidae, Paraonidae, Questidae, and Scalibregmatidae (Fig. 63). The Ctenodrilidae groups with the Aeolosomatidae, Parerogodrilidae and Potamodrilidae in the *A/Pec* analysis (Fig. 63) and with the Acrocirridae, Cirratulidae, Fauveliopsidae, Flabelligeridae, Poeobiidae and Sternaspidae in the *A/Pwc* analysis (Fig. 65). In the *Mc* analysis, the position of the Ctenodrilidae is unresolved (Fig. 66).

The Protodrilidae, Polygordiidae, Protodriloididae and Saccocirridae form a clade in both of the A/P complete analyses (Figs 63, 65), but they are part of a basal polytomy in the *Mc* analysis (Fig. 66). In the *A/Pwc* analysis, the clade containing the Polygordiidae, Protodrilidae, Protodriloididae and Saccocirridae falls within the clade having grooved palps (Fig. 65), whereas in the *A/Pec* analysis, the taxa having grooved palps form two distinct groups (Fig. 63).

The Aeolosomatidae, Parergodrilidae and Potamodrilidae form a clade in both A/P complete analyses (Figs 63, 65). In the *A/Pec* analysis, this clade is plesiomorphic with respect to virtually all polychaetes, but they are part of a basal polytomy in the *Mc* analysis (Fig. 66). In the *A/Pec* analysis (Fig. 63), the Psammodrilidae appears as sister group to a clade that comprises the (Arenicolidae Capitellidae Maldanidae). In the *A/Pwc* analysis, these taxa form a grade immediately basal to the taxa having grooved palps (Fig. 65). In the *Mc* analysis, the Psammodrilidae is part of a basal polytomy (Fig. 66).

segmented worms (Fig. 66). In all three complete analyses, most of the pelagic and commensal polychaete families with a hypertrophied muscular axial pharynx group with other taxa identified by this feature. The exception is the Myzostomidae. While in the *A/Pwc* and *Mc* analyses, the myzostomes are found amongst other taxa with a hypertrophied axial pharynx (Figs 64–66), in the *A/Pec* analysis, they form a clade with the Spintheridae that is basal with respect to most 'polychaete' taxa (Figs 62, 63). The Spintheridae otherwise appears as a basal member of the clade that includes taxa with a hypertrophied axial or ventral pharynx (Figs 64, 65) or as sister group to the (Amphinomidae Euphrosinidae) in *Mc* analyses (Fig. 66).

Discussion

Status of the Pogonophora

The most significant result of the analyses presented here is that the phylum Pogonophora (including the former phylum Vestimentifera; see Rouse & Fauchald 1995) clearly appears within the traditionally formulated Annelida, and in fact represents a derived clade of the Polychaeta. The suggestion that the Pogonophora are annelids is not new (see Rouse & Fauchald 1995 for a review). There are also clear precedents that pogonophores could be polychaetes; one of the earliest descriptions placed them as a subfamily of the Sabellidae (Uschakov
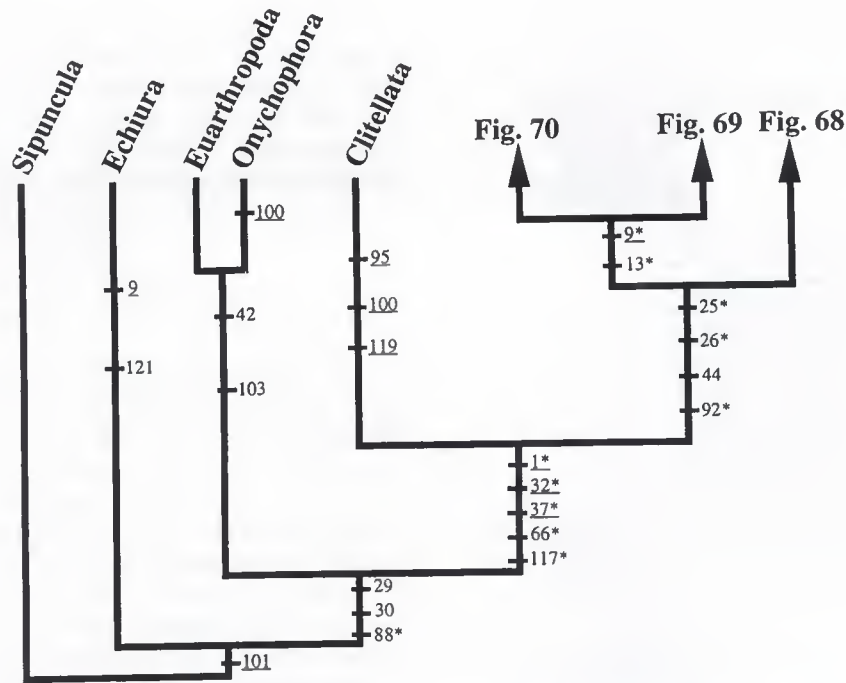
Fig. 67. Basal region found in all three trees derived from SW for the *A/Pwr* analysis (Fig. 59). The three major clades of the Polychaeta are shown in Figs 68–70. Only unambiguous transformations are shown. Areas of multiple possible transformation are not shown for characters A/P5, A/P102 and A/P105. Characters in plain text show no homoplasy. * indicates the character reverses subsequently above the supported node. Underlined characters show homoplasy through convergence or parallelism. For character description, see Appendix I.

Fig. 67
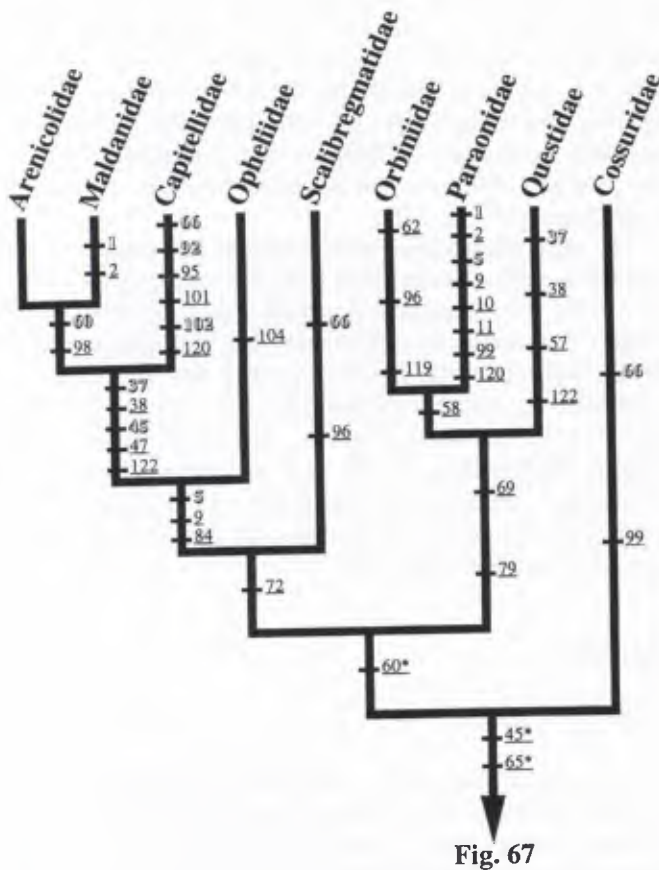
Fig. 68. One of the major polychaete clades found in all three trees derived from SW for the *A/Pwr* analysis (Fig. 59). Only unambiguous transformations are shown. Areas of multiple possible transformation are not shown for characters A/P56 and A/P65. Underlined characters show homoplasy through convergence or parallelism. Characters in 'outline' text are reversals. * indicates the character reverses subsequently above the supported node. For character description, see Appendix I.

1933). However, the last clear statement that they were polychaetes (though a polyphyletic assemblage), can be found in Hartman (1954a). Until the recent statements by Bartolomaeus (1995), Nielsen (1995) and Rouse & Fauchald (1995), the debate about their position has mainly concerned (1) whether they were 'protostomes' or 'deuterostomes' or (2) whether they should be regarded as one phylum or two (see Rouse & Fauchald 1995: 271–273).

Rouse & Fauchald (1995: 287) suggested "the Pogonophora will be found to fall within the Polychaeta, close to the sabellid/terebellid clade of polychaetes". This is largely reflected in the results of all analyses presented here. Bartolomaeus (1995) also advocated a sabellid/terebellid relationship for the Pogonophora and in fact showed a tree with the Pogonophora as sister group to a Sabellida (comprising the Sabellidae and Serpulidae). He then placed the Terebellida (presumably the Ampharetidae, Pectinariidae, Terebellidae and Trichobranchidae) as sister group to the Pogonophora/Sabellida clade, based on the shared presence of uncini. Bartolomaeus (1995) argued that the Pogonophora is the sister group to his Sabellida based on the presence of a pair of anterior nephridia. However, this cannot be unequivocally accepted since such an anterior pair of nephridia is found in seven other families: the Acrocirridae, Cirratulidae, Ctenodrilidae, Flabelligeridae, Poeobiidae, Sabellariidae and Sternaspidae (see Appendix IV), and this was not discussed by Bartolomaeus (1995). In the present analyses, this feature can be a synapomorphy for the Pogonophora, Sabellidae, Serpulidae and Sabellariidae (Figs 71, 72). However, in the context of all available evidence, rather than the few characters considered by Bartolomaeus (1995), it is a homoplastic feature. Based on *Mr* and *A/Pwr* trees, the results also suggest that the homology of
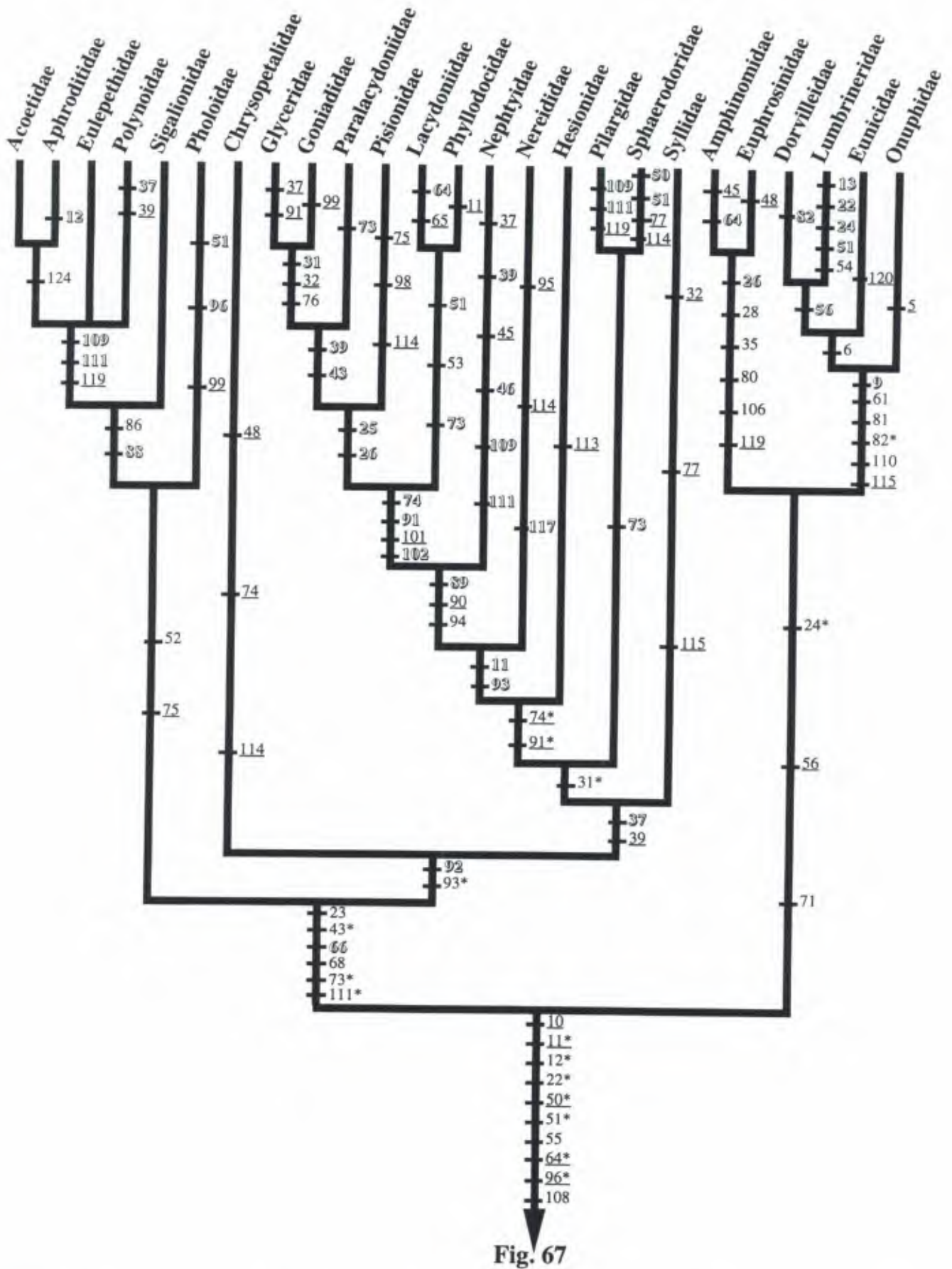
Fig. 67

Fig. 69. One of the major polychaete clades found in all three trees derived from SW for the *A/Pwr* analysis (Fig. 59). Only unambiguous transformations are shown. Areas of multiple possible transformation are not shown for characters A/P32, A/P33, A/P41, A/P46, A/P96, A/P98, A/P101, A/P102, A/P109, A/P113 and A/P115. Characters in plain text show no homoplasy. Underlined characters show homoplasy through convergence or parallelism. Characters in 'outline' text are reversals. * indicates the character reverses subsequently above the supported node. For character description see Appendix 1.
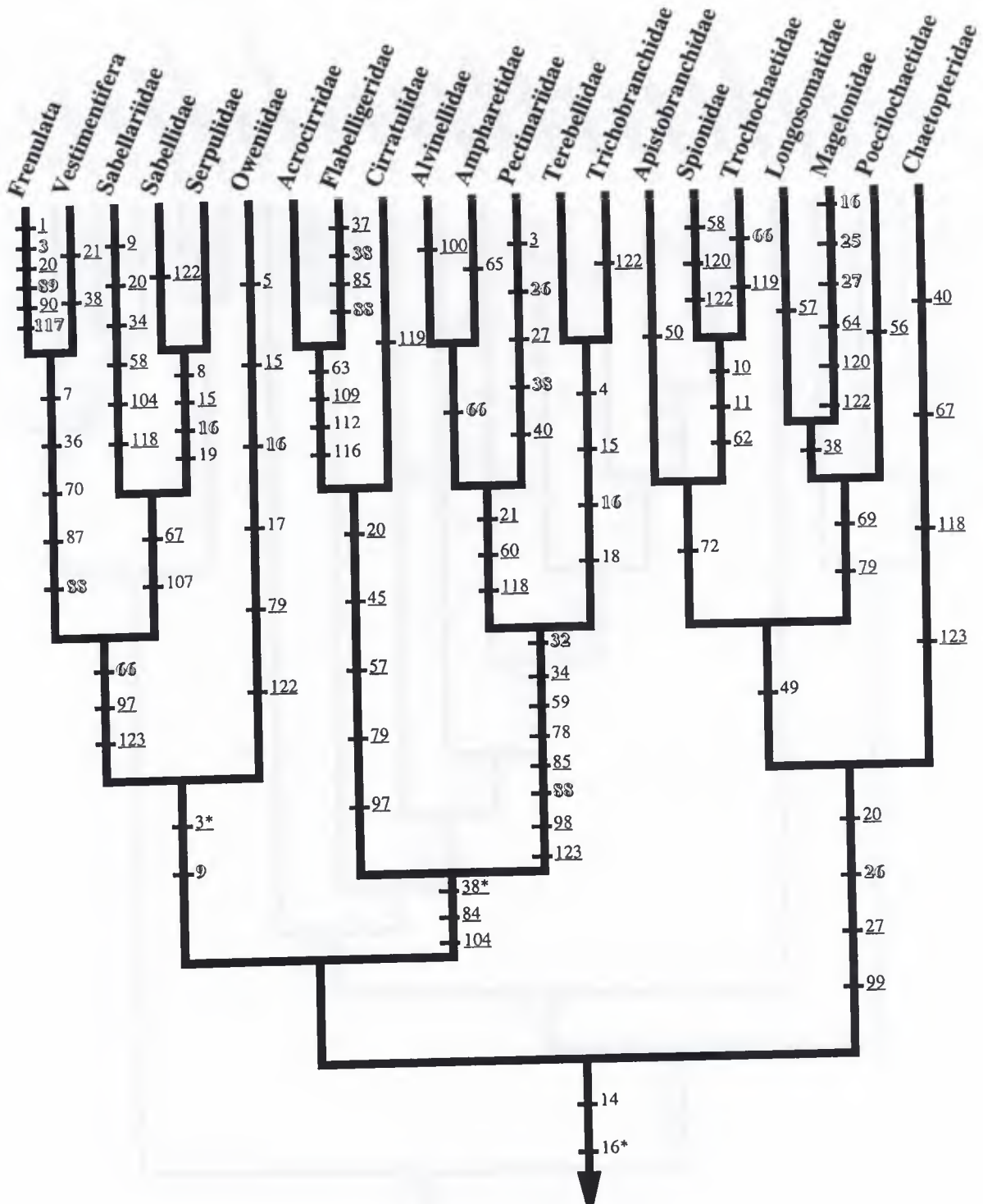
Fig. 67

Fig. 70. One of the major polychaete clades found in all three trees derived from SW for the *A/Pwr* analysis (Fig. 59). Only unambiguous transformations are shown. Areas of multiple possible transformation are not shown for characters A/P1, A/P32, A/P37, A/P40, A/P47, A/P60, A/P65, A/P69, A/P92 and A/P119. Characters in plain text show no homoplasy. Underlined characters show homoplasy through convergence or parallelism. Characters in 'outline' text are reversals. * indicates the character reverses subsequently above the supported node. For character description, see Appendix I.

uncini, as suggested by Bartolomaeus (1995), has to be rejected. However, the support for the branches under discussion here is relatively weak, and the topology proposed by Bartolomaeus (1995) can be virtually seen in Fig. 57 for *A/Per* trees and may well prove to be correct.

Further investigation of the relationships among the taxa that have grooved palps is clearly required, and detailed structural analyses, as performed by Bartolo-

maeus (1995), are essential. As an example of the need for further study, two decisions outlined in Appendix IV concerning the Pogonophora could have some influence on their systematic position within the Polychaeta. It is possible to interpret them as having a heart body and a gular membrane (see Appendix IV), though a conservative approach was taken, and they were scored absent for these features. If pogonophores are found to have a heart body
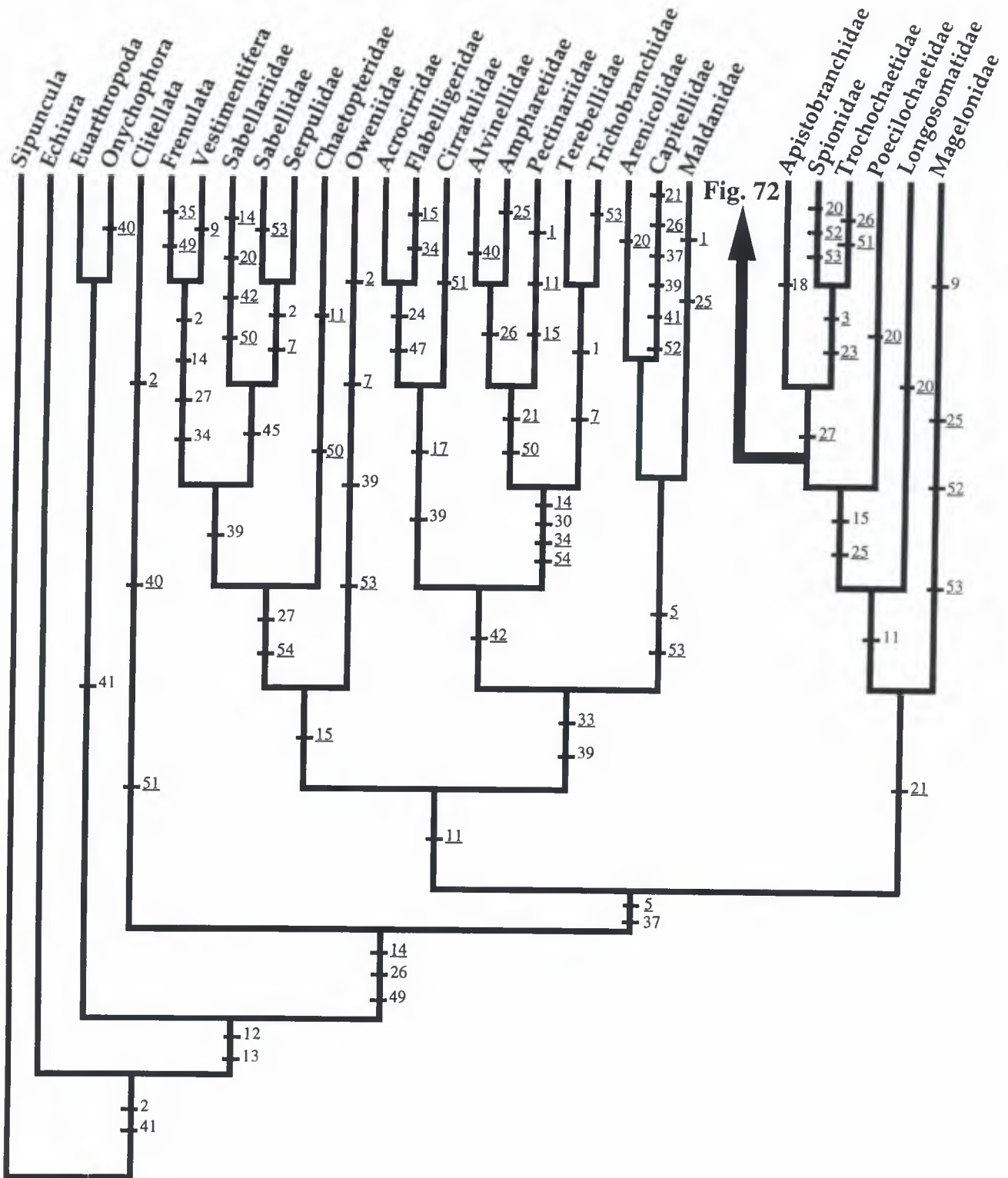
Fig. 71. Basal region found in one of 440 trees derived from SW for the *Mr* analysis (Fig. 61). The remaining major clade of the Polychaeta is shown in Fig. 72. Only unambiguous transformations are shown. Characters in plain text show no homoplasy. * indicates the character reverses subsequently above the supported node. Underlined characters show homoplasy through convergence or parallelism. For character description, see Appendix 1.

and/or a gular membrane, then the pattern relationships among the taxa discussed above could alter, as would the transformation series of features such as the anterior pair of nephridia and uncini.

The Pogononophora should now be reclassified as members of the clade Sabellida (see below). Since the name Pogonophora is misleading at this level, the name of the group should revert to that of the first family group

name originally formulated for members of the group, that of Siboglinidae Caullery, 1914. Note that Rouse & Fauchald (1995) made an error in suggesting that the more recent name Lamellisabellidae Uschakov, 1933 should be used for the Pogonophora if it proved to fall within the Polychaeta. The current classification of the Pogonophora is thus made redundant, and major revision is required. All currently named families of Pogonophora
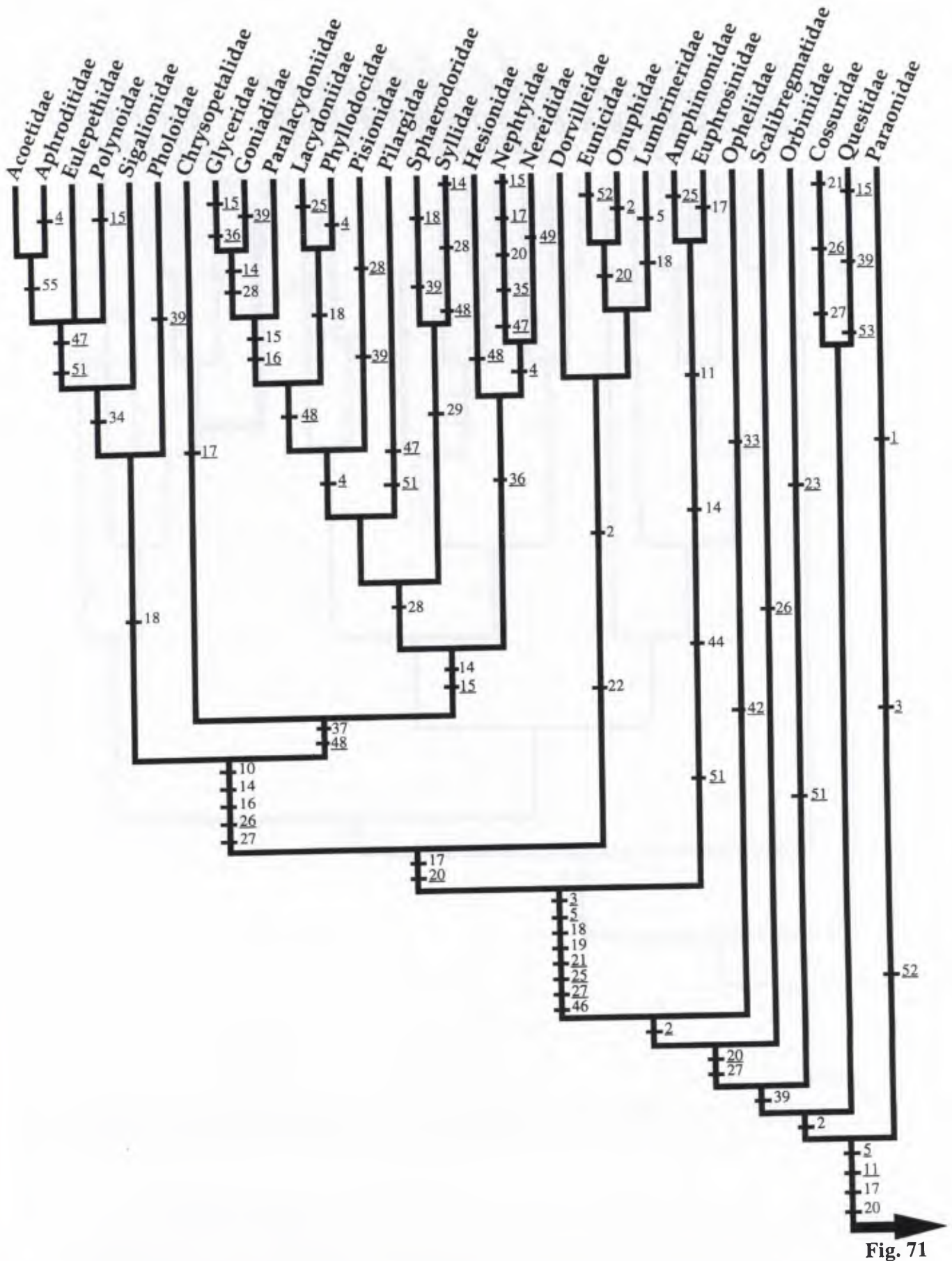
Fig. 71

Fig. 72. Clade of polychaetes not shown in Fig. 72 from one of 440 trees derived from SW for the Mr analysis (Fig. 61). Only unambiguous transformations are shown. Characters in plain text show no homoplasy. * indicates that the character reverses subsequently above the supported node. Underlined characters show homoplasy through convergence or parallelism. For character description, see Appendix I.

become synonyms of the Siboglinidae. The Vestimenti-fera also fall within the Siboglinidae since it was shown (Rouse & Fauchald 1995) that Jones (1985) was erroneous in separating this group from the Pogonophora. The sister group for the 'vestimentiferans' probably lies among the former family Sclerolinidae, as implied by Southward (1993). A new hierarchical classification subsidiary to the clade name Siboglinidae will have to be constructed, and a cladistic analysis of the group is clearly necessary.

Position of other problematic taxa

Another interesting result concerns the placement of the Aeolosomatidae and Potamodrilidae. While usually associated with the Clitellata (see Rouse and Fauchald 1995), the results here are the first to suggest that they fall within the Polychaeta, though admittedly, their placement in the group is uncertain (see below). Moon *et al.* (1996) presented an analysis of molecular sequence data based on 18S ribosomal RNA for a mollusc, a polychaete (*Glycera americana*, a glycerid), three clitellates and a species of *Aeolosoma*. They found 79 informative sites, used phenetic and parsimony analyses and rooted their trees using the mollusc to infer that *Aeolosoma* was the sister group to the clitellate clade. This contradicts the results shown here and lends support to previous hypotheses about the position of the Aeolosomatidae. However, further sampling of polychaetes across a range of taxa is probably advisable to test whether the Aeolosomatidae and Potamodrilidae are clitellates or polychaetes.

The unusual morphology of myzostomes has been emphasised in the past, while features such as the presence of parapodia, cirri, aciculae and a hypertrophied axial pharynx have been disregarded (see Rouse & Fauchald 1995). The placement shown on Figs 65, 66 with the Myzostomidae as a member of the clade having a hypertrophied axial pharynx was foreshadowed in Rouse & Fauchald (1995). However, the position of the Myzostomidae within this clade cannot be ascertained with any confidence at this time, and molecular sequence data may be required. Other pelagic or commensal families that have a hypertrophied axial pharynx may also require such studies, though further detailed morphological studies undoubtedly would be helpful. The grouping of the Myzostomidae and Spintheridae as basal polychaetes in the *A/Pec* analysis (Figs 62, 63) probably should be disregarded since both groups are symbiotic, and their basal position can be largely regarded as losses appearing as primary absences (see below).

The position of the Polygordiidae, Protodrilidae, Protodriloididae and Saccocirridae in the A/P complete analyses provides some evidence for the hypothesis by Purschke & Jouin (1988) that this group is monophyletic and has a relationship with spioniform taxa. However, in both A/P complete analyses, the cirratulids and other taxa are closer to the spiomorphs, and for this reason, the position of the four families should still be regarded as uncertain. Since their first description, the systematic position of the Psammodrilidae has been somewhat isolated (Swedmark 1958). The recent placement of the

group as close to arenicolids and maldanids by Bartolomaeus (1995) is supported in the A/P analyses and should be further investigated.

In the A/P complete analyses, the Diurodrilidae and Histriobdellidae appear as basal clade. However, this placement is almost certainly incorrect. The morphology of the jaws of the Histriobdellidae is so similar to that of eunicemorph polychaetes that it is arguably unlikely to have arisen convergently (Mesnil & Caullery 1922). The genus *Diurodrilus* was originally placed in the Dinophilidae before being placed into its own family (Kristensen & Niilonen 1982). However, the unusual features of the group appear to have been emphasised by Kristensen & Niilonen (1982), and similarities with *Dinophilus* were disregarded. *Dinophilus* is now regarded as a derived member of the Dorvilleidae (Eibye-Jacobsen & Kristensen 1994), and *Diurodrilus* also may belong in this family. Molecular sequence data may be required to properly resolve the placement of these taxa.

The placement of the Diurodrilidae and Histriobdellidae in all complete analyses lends support to the idea that organisms that show extensive loss of features may be placed inaccurately. The Diurodrilidae and Histriobdellidae are unusual among polychaetes in lacking chaeta and all parapodial structures. This is a drawback of including taxa in an analysis simply because they all have the taxonomic rank of family. However, it would appear that the losses have to be extreme since most 'simple' taxa are placed close to their generally proposed sister taxa (see below).

New classification

Given the variability in results from the different coding methods, the choice of classification is not straightforward. However, the current state of polychaete classification is clearly unsatisfactory and considered use of the analyses conducted here would be an improvement on what is currently available. Nevertheless, it is with some reluctance that a new classification is proposed since this study must be regarded as one of the initial steps in a new phase of polychaete systematics. While the placement of many of the taxa in the complete analyses is not surprising and matches current ideas (e.g. Fauveliopsidae, Poeobiidae, pelagic taxa with hypertrophied axial pharynges), others have placements that are certainly incorrect (e.g. Histriobdellidae, Diurodrilidae are most likely members of the clade having a hypertrophied ventral pharynx, not basal polychaetes). Therefore, the new classification is based on a restricted analysis, and the taxa that were excluded are placed within the taxon to which they are most likely to belong. However, the overall topology of the complete analyses also differs significantly from the restricted analyses, and this should be kept in mind with reference to the classification presented here. For example, the position of the clades (Arenicolidae Capitellidae Maldanidae), (Acrocirridae Cirratulidae Flabelligeridae) and Oweniidae differs markedly between the complete and restricted analyses using *A/Pw* coding.

Given that a restricted analysis is to be used for the classification, the issue is then which of the coding methods

to utilise. *A/Pe* coding is clearly unsatisfactory because of the marked hierarchical linkage of characters. *A/Pw* coding also suffers from this problem, but an attempt has been made to control the problem. *Multistate* coding suffers from the subjectivity of the original character construction, the lack of testing of the homology assumptions and other problems pointed out by Pleijel (1995). So, while essentially an arbitrary decision, the *A/Pwr* analysis seems to be the best solution, and this is used for the basis of this new classification.

The taxon Articulata is supported by essentially the same apomorphies as identified by Rouse & Fauchald (1995), namely the presence of segmentation and longitudinal muscle bands. The Articulata is also unequivocally supported in *A/Pwr* analysis by the presence of a straight gut (Fig. 67). The Echiura is sister group to the Articulata in all restricted analyses. Nielsen (1995) and Eibye-Jacobsen & Nielsen (1996) include the Echiura in the Annelida on the basis that they have lost segmentation and that chaeta must have evolved once. The results of the present analyses suggest that chaetae could have evolved twice, once in the Echiura and once in the Annelida, or that the presence of such structures is plesiomorphic for the Articulata and they have been lost in the Arthropoda. There is no evidence to support the contention by Nielsen (1995) that the Echiura have lost segmentation, but since the branch support for the Articulata (and Annelida) is weak, further investigation into the position of the Echiura should be pursued using molecular sequence data.

In all restricted analyses, the traditionally formulated Annelida is monophyletic (though weakly supported) and, for the time being, is accepted as a valid taxon. It comprises two clades, the Clitellata and Polychaeta, though the monophyly of the latter is not well supported. Nielsen (1995: 134) proposed that, with regards to the Clitellata, "it could be more useful to regard the polychaete family Capitellidae as the sister group instead of the whole polychaete 'class'". This proposal is not supported in any of the analyses performed here. Nielsen (1995) argues that the restriction of reproductive organs and occurrence of hermaphroditism in some capitellids are homologous with the clitellate reproductive condition. However, many capitellids have numerous segments that are fertile, e.g. *Dasybranchus caducus* (Eisig 1887; Goodrich 1945), extreme reduction of segments with gametes occurs in only a few capitellids, and hermaphroditism in the group is even rarer. The organization of the reproductive system in this group cannot be regarded as homologous with the Clitellata at this time, and a cladistic analysis of the Capitellidae is needed to determine the plesiomorphic reproductive condition for the group. Nielsen's (1995) argument actually implies that the Capitellidae is paraphyletic by exclusion of the Clitellata. The possibility that the Clitellata has a sister group amongst the polychaetes may have to be resolved on molecular sequence data.

The hypothesis that the Clitellata is the sister group to the Arthropoda, as reviewed in Rouse & Fauchald (1995), may be discounted on present evidence. Admittedly, the characters used in this study were selected for resolving amongst polychaete taxa and, given the inadequacies of available coding methods, the possibility of a paraphyletic Annelida deserves further investigation. The basic classification is presented on the tree shown in Fig. 73 and in an indented form in Fig. 74.

The Polychaeta is divided into the clades Palpata and Scolecida. The former term is a new name based on the synapomorphy of the presence of palps. Scolecida is a name derived from the name Scoleciformia introduced by Benham (1896) and little used since Goodrich (1945). The Scolecida includes many of the taxa initially placed in the Scoleciformia by Benham and subsequent workers and is derived from the Greek *skolex* for worm. The Palpata is divided into the Aciculata and Canalipalpata. The Aciculata is a strongly supported clade, and the name refers to one of the synapomorphies for the group, the presence of aciculae. The Canalipalpata is not strongly supported, but the name refers to one of the group's synapomorphies, the presence of grooved palps.

The Aciculata is divided into the clades Phyllodocida and Eunicida. These are names that are currently in common use (see Fauchald & Rouse 1997), though the formulation of the Eunicida now includes the Amphinomidae and Euphrosinidae. The Canalipalpata has three major clades whose relationships are unresolved using the *A/Pwr* analysis. They are given the names Sabellida, Spionida and Terebellida. These are names currently in use. The formulation of the Spionida is similar to current usage, but the other two names have somewhat radical memberships. The Sabellida is now formulated to include the Siboglinidae and Oweniidae. The Terebellida includes the five families usually associated with the name but, additionally, the taxa Acrocirridae, Flabelligeridae and Cirratulidae.

Most of the 29 families that were excluded from the restricted analyses can be easily placed in the above classification. The results of the complete analysis show that the inclusion of paraphyletic taxa is not particularly problematic in general (see Rouse 1997). The families that were proposed to be paraphyletic generally have their excluded members placed in close proximity, e.g. Ctenodrilidae with Cirratulidae; Poeobiidae and Fauveliopsidae with the Flabelligeridae. Based on previous ideas and their placement in the complete analyses, 16 families are classified as follows:

1. The families Alciopidae, Ichthyotomidae, Iospilidae, Lopadorhynchidae, Myzostomidae, Nautillienellidae, Pontodoridae, Typhloscolecidae and Tomopteridae, are all members of the Phyllodocida.

2. The Oenonidae and Hartmaniellidae are members of the Eunicida.

3. The Ctenodrilidae, Fauveliopsidae, Poeobiidae and Sternaspidae all form a clade with the Acrocirridae, Cirratulidae and Flabelligeridae in the Terebellida. The placement of the first three taxa is unsurprising, and Dahl (1955) also argued for a close relationship between the Sternaspidae and Flabelligeridae. The possibility that sternaspids may have palps (see Sluiter 1882) should be investigated further.

4. The Uncispionidae falls within the Spionida.

The remaining 13 excluded families are more difficult to classify. As indicated above, the Histriobdellidae and
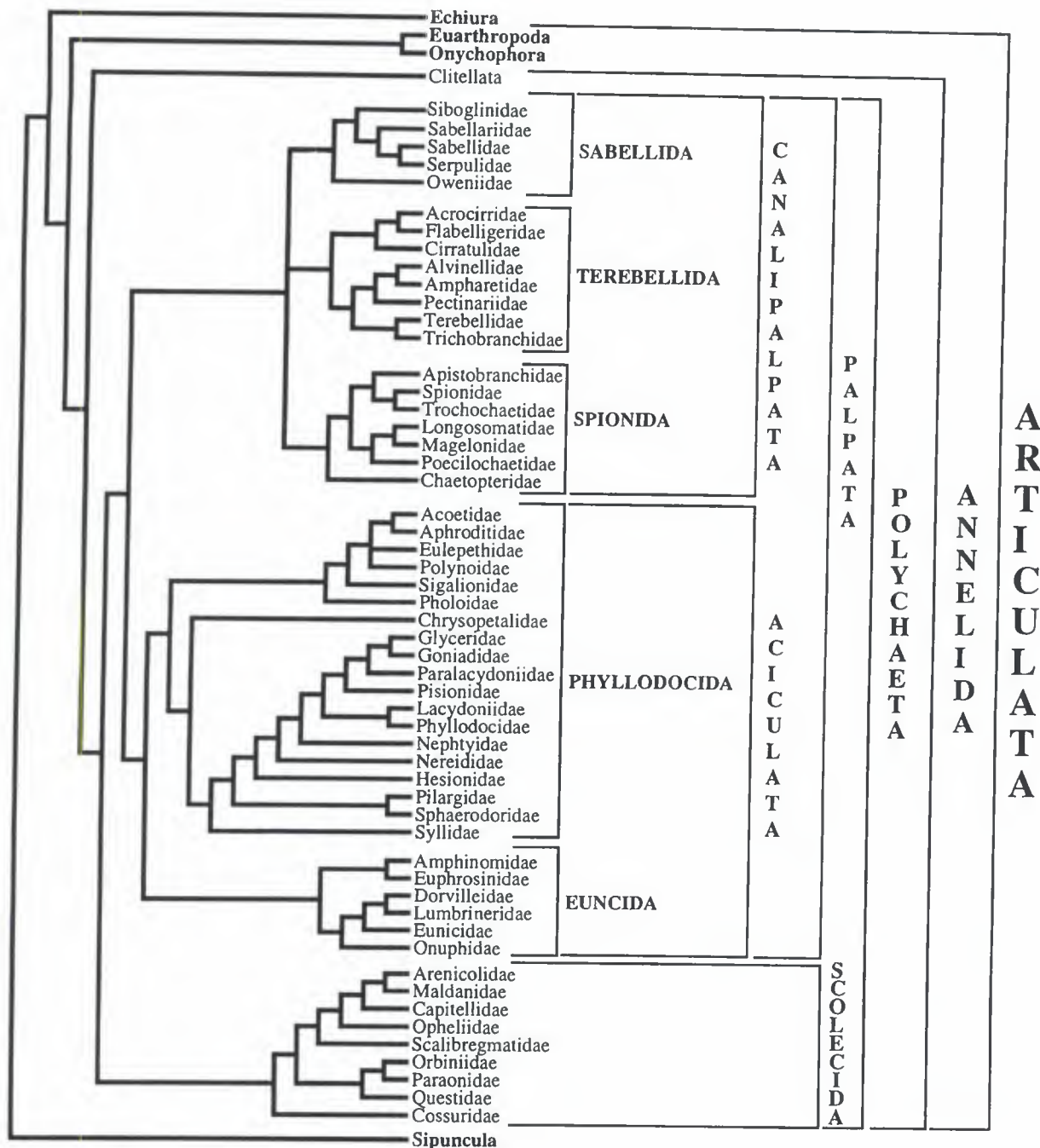
Fig. 73. Basic classification of the taxa in these analyses based on the trees derived from SW for the *A/Pwr* analysis (Fig. 59). The 29 taxa excluded from this analysis are placed within clade names shown here based on the *A/Pwc* analysis and arguments in the text (see Appendix V for the classification of excluded taxa). Note that the Pogonophora (and Vestimentifera) are now referred to by the name Siboglinidae, and this family is a member of the Sabellida.

Diurodrilidae are most likely to be members of the Eunicida, rather than the most plesiomorphic clade of the Annelida, as suggested by Figs 62–65. They are placed as Eunicida *incertae sedis*. The position of the Aeolosomatidae, Potamodrilidae, Parerogodrilidae cannot be resolved on current evidence. They are members of the Polychaeta but otherwise are best regarded as *incertae sedis*. The Psammodrilidae are also placed as Polychaeta *incertae sedis*, though a relationship with the arenicolids and maldanids should be assessed. In the complete analyses, the Aberrantidae, Nerillidae, and Spintheridae mainly fall with taxa in the Aciculata, though the former two taxa lack such structures. All three families are left as *incertae sedis*

in the Aciculata pending further investigation. The clades (Polygordiidae, Protodrilidae, Protodriloididae and Saccocirridae) are classified within the Canalipalpata, though they are left as *incertae sedis* in this clade. The prediction by Purschke & Jouin (1988) that they should be grouped with spiomorph taxa, i.e. Spionida, deserves further investigation but cannot be supported on the present results.

In keeping with the opinions expressed in Rouse & Fauchald (1995) regarding the inadequacy of the current nomenclatural system no Linnaean categories (class, order, etc.) are used here. The emphasis is instead placed on naming monophyletic taxa. The Latin endings to the names should not be interpreted as evidence for any

Articulata

   Arthropoda

   Annelida

      Clitellata

      Polychaeta

         Scolecida

         Palpata

            Canalipalpata

               Sabellida

               Spionida

               Terebellida

            Aciculata

               Phyllodocida

               Euncida
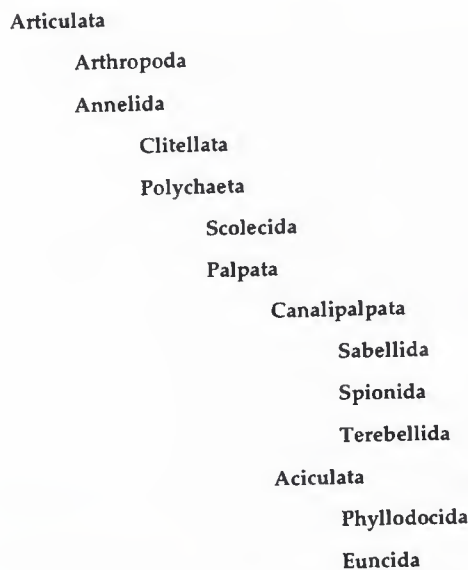
Fig. 74. Indented classification of taxa considered in this analysis based on Fig. 73. Note that Linnaean categories are avoided wherever possible in this study.

Linnaean category; rather, they are to provide simple formal taxon names that avoid any confusion with vernacular usage. Given that this classification probably will be revised considerably, an extensive taxonomy is not provided here. Also, few new names are provided, and previously used taxa are reformulated wherever possible. This results in substantially fewer groupings above the 'family' level than the most recent classifications, e.g. 17 orders of Fauchald (1977) or 25 orders of Pettibone (1982), and a better hierarchical structure is present. There are problematic taxa that are difficult to place on currently available evidence. The best solution to this is to leave them unresolved, rather than to give them a high rank. All 83 currently acceptable families of the Polychaeta are shown in Appendix V.

Transformations

Palps. Orrhage (1966, 1980, 1991, 1993, 1995, 1996) has provided convincing argumentation to support initial hypotheses that all forms of 'palps' are homologous structures, and this is largely supported in these analyses, though the implications for the evolution of palps vary with the coding method.

In the restricted analysis using multistate coding, the presence of palps in general is a synapomorphy for the Polychaeta, being subsequently lost in the clade (Arenicolidae Capitellidae Maldanidae), the family Lumbrineridae, and the grade Paraonidae, Questidae, Orbiniidae, Cossuridae and Opheliidae. The clade Aciculata shows the reappearance of palps, which suggests that ventral sensory palps may not be homologous with grooved palps (Figs 71, 72). However, the fact that taxa such as the Scalibregmatidae and Paraonidae show signs of palpal innervation (Orrhage 1993), though no actual palps, supports the possibility that all palps or, minimally, palpal nerves are homologous. In *A/Per* and *A/Pwr* analyses, the presence of palps in general is a synapomorphy for the Palpata (e.g. character 13 in Fig. 67) with a subsequent loss in the

Lumbrineridae, and this transformation supports Orrhage's arguments that all palps are homologous. The presence of grooved palps is a synapomorphy for the Canalipalpata (e.g. character 14 in Fig. 70). The homology of the various forms of grooved palps is also supported in the *A/Per* and *A/Pwr* analyses, with peristomial palps appearing to be the plesiomorphic condition in the clade. Further developmental studies of taxa such as the Terebellidae, Oweniidae, Magelonidae would be of considerable interest.

Stomodaeum. The suggestion by Purschke & Tzetlin (1996) that dorso-lateral folds are a plesiomorphic feature of the Polychaeta is supported by the present results. In fact, if the argument that they are plesiomorphic for clitellates (Purschke & Tzetlin 1996: 47) is accepted (as it is here), then the presence of dorso-lateral folds is a synapomorphy for the Annelida (e.g. character 66, Fig. 67; character 26, Fig. 71). Purschke & Tzetlin (1996) also suggested that dorso-lateral folds have been lost a number of times within the Polychaeta, a hypothesis with which the trees shown here support. Dorso-lateral folds have been lost at least six times, depending on the form of coding used.

Dales (1962, 1977) and Purschke & Tzetlin (1996) have argued that a ventral buccal organ represents the primitive stomodaeal condition for the Polychaeta. In the *A/Per* and *A/Pwr* trees, the coding for the various sorts of buccal organs is such that there is no plesiomorphic polychaete buccal organ feature, i.e. the ancestral node for the Polychaeta shows all 0s for stomodaeum characters. One of the supposed problems with A/P coding perceived by Meier (1994) was that such all '0' optimizations are pseudoparsimonious. However, as pointed out by Pleijel (1995), all this really means is that the ancestor is estimated to have none of the specified states. The reason that such a result was obtained in *A/Per* and *A/Pwr* trees may be that, while there are clearly four different types of buccal organs in polychaetes, there is little evidence available for assessing any homology among these forms. Further assessment and study of the ontogeny of the stomodaeum in various polychaetes are clearly required, particularly with regards to the potential homology of the ventral buccal organ structure of the Eunicida with other ventral buccal organs.

In the restricted analyses for each form of A/P coding, a ventral buccal organ appears between two and four times independently. These results do not support the suggestion by Dales (1962) and Purschke & Tzetlin (1996) that the majority of ventral buccal organs in polychaetes are homologous. However, in multistate coding, ventral buccal organs do represent the plesiomorphic condition for the Polychaeta and have subsequently transformed into various other forms of polychaete buccal organs. This result shows several similarities with the scheme presented by Dales (1977) for the evolution of the polychaete stomodaeum.

Nephridia, segmental organs and circulatory systems. There are several issues concerning nephridia and circulation that can be discussed in the light of the finding represented in this paper. These concern:

1. The adequacy of Goodrich's (1945) terminology describing nephridia and gonoducts (segmental organs).

2. The homology of structures termed metanephridia and protonephridia and the transformation series between them.

3. The association of nephridial systems with circulation patterns as proposed in a model by Ruppert & Smith (1988).

Assessment of Goodrich's (1945) hypotheses. The accuracy of Goodrich's (1900, 1945) terminology to describe 'segmental organs' should be assessed in the light of homology. Currently, there is no consensus on the validity of this terminology, though it has been rejected as erroneous by Bartolomaeus (1989) or ignored in major reviews by Ruppert & Smith (1988), Smith & Ruppert (1988), and Bartolomaeus & Ax (1992). These authors have simply used the terms protonephridia and metanephridia. Others have used Goodrich's (1945) terminology but questioned the placement of taxa in his classification (e.g. Smith 1988).

Based on observations that clitellates and certain members of the Capitellidae have separate nephridia and gonoducts, Goodrich (1945) argued that this was the primitive annelid condition and that fusion of the two systems had occurred in various ways among polychaete taxa. While this argument is not compelling, the evidence for fusion of different tissues to form segmental organs is strong. The theoretical basis of Goodrich's (1945) monograph rested on the observation that, in polychaetes in particular, mesodermal elements and ectodermal (or ectomesodermal) nephridia could fuse to form single structures. Nephridia can have an ending in the body that may be closed (= protonephridia) or have an opening (= metanephridia) termed a nephrostome. Mesodermal elements derived from the coelomic wall can form distinct funnels or ducts to the exterior, termed coleomostomes and coelomoducts, respectively, by Goodrich (1945). Goodrich (1900: 742) defined nephromixia as structures resulting from the fusion of the two types of tissue. Where nephromixia occur, Goodrich (1945: 119) classified them into three groups: protonephromixia, metanephromixia and mixonephridia. *Protonephromixia* have mesodermal components grafted on to the canal of the protonephridia. *Metanephromixia* was a term to be used when there was clear morphological evidence that coelomostomes have been added to open nephrostomes and *mixonephridia* for when the coelomic ends of the nephridia were completely lost and fused with coelomostomes. The other feature distinguishing metanephromixia appears to be that they do not appear until sexual maturity, whereas mixonephridia form much earlier. However, as Goodrich (1945: 119) himself argued, the line between metanephromixia and mixonephridia is difficult to draw. The terminology was briefly reviewed by Smith (1988) who argued that the mixonephridia of terebellids should be classified as metanephromixia. While Smith (1988) was correct in interpreting Goodrich's (1945) definition of metanephromixia, the results shown here indicate that it would be incorrect to classify terebellid segmental organs as metanephromixia and that what is probably needed is additional terminology (see below).

A more serious criticism of Goodrich (1945) was put forward by Bartolomaeus (1989) and Bartolomaeus & Ax (1992) who rejected the idea that there is a mesodermal component to polychaete segmental organs and hence ignored Goodrich's terminology. Bartolomaeus (1989) argued that the 'protonephromixia' of the phyllodocid *Anaitides mucosa* had open funnels into the coelom with no mesodermal component. They are, in a sense, both protonephridial and metanephridial. In fact, Bartolomaeus & Ax (1992: 39) actually called the segmental organs found in *A. mucosa* metanephridia. Bartolomaeus & Ax (1992) also showed that the pholoid *Pholoe minuta* developed metanephridia through a protonephridial stage and used this as evidence to argue that there is no coelomic component to polychaete segmental organs. However, Goodrich (1945) was perfectly aware that metanephridia passed through a protonephridial stage during development and described several cases. There is nothing in the observations of Bartolomaeus & Ax (1992) to contradict Goodrich's (1945) terminology. *Pholoe minuta* may add a mesodermal component to the metanephridial at sexual maturity, thus forming a metanephromixium or form a mixonephridium at a juvenile stage not investigated by Bartolomaeus & Ax (1992).

Bartolomaeus (1989: 31) rejected Goodrich's (1900, 1912b, 1945) conclusions on the development of segmental organs in alciopids, in which the protonephromixia had a mesodermal component, as "probably a misinterpretation", though Goodrich is explicit in his drawings and observations. Bartolomaeus (1989) also suggested that the differential staining used by Goodrich (1900, 1945) to distinguish mesodermal from ectodermal tissue could be misleading and cited three studies of polychaetes where no mesodermal contribution to the segmental organs had been found; Lillie (1906) in *Arenicola cristata* (Arenicolidae), Rice (1980) in two *Polydora* species (Spionidae), and Stecher (1968) in *Pisione remota* (Pisionidae). Based on this line of evidence, Bartolomaeus (1989) argued that polychaete segmental organs are completely ectodermal structures.

However, there is ample evidence of mesodermal contribution to polychaete segmental organs, and dismissing Goodrich's studies and ideas is premature, particularly based on the papers cited by Bartolomaeus (1989). For example, Goodrich (1945) himself discussed the findings of Lillie (1906) and his own studies on the development of segmental organs in *Arenicola*, and concluded that there is a mesodermal component, justifying the description of them as mixonephridia. Bartolomaeus's (1989) characterization of the 'nephridia' of *Arenicola* as derived from solid 'anlagen' is misleading, and Goodrich (1945: 206–210, fig. 52) and Lillie (1906) should be consulted. Lillie (1906: 388, 390) specifically refers to a component of the 'nephrostome' as being derived from the septum (i.e. mesoderm). Rice (1980: 182) used the term nephrostome for the internal opening of the segmental organs of two spionid species "rather than coelomostome because the independent origin of this structure has not been proven". This is hardly evidence for the organs being ectodermal structures. While evidence is provided by Stecher (1968) for an ectodermal origin of segmental organs in *P. remota*, Aiyar & Alikunhi (1940) describe the development of the genital funnels from mesodermal tissue in another pisionid,

Pisionidens indica. The evidence for completely ectodermal segmental organs in all polychaetes thus appears to be fairly weak. In contrast, there are observations that support Goodrich's (1945) terminology.

Meyer (1887, 1888, 1901) described in detail the development of segmental organs in terebellid and serpulid species and clearly stated that the nephridial ducts are retroperitoneal (i.e. ectodermal or ectomesodermal) but that the funnels are clearly peritoneal (= mesodermal). His emphasis on the two origins for the segmental organs is very plain and cannot be disregarded. Combined with Goodrich's own large body of observations and those of Lillie (1906), it is clear that the issue of the origin and structure of polychaete segmental organs is by no means resolved. The suggestion by Bartolomaeus (1989) that 'protonephromixia' are actually derived from a single tissue source is interesting but does not mean that Goodrich's terminology should be discarded. Certainly, the co-existence of metanephridia and protonephridia in the same 'organ', as proposed by Bartolomaeus (1989), is interesting and deserves further study. If the suggestion by Bartolomaeus (1989) for *A. mucosa* is confirmed and is also found in other taxa, then instead of describing segmental organs with a protonephridium and a coelomostome fused, the term protonephromixia could be redefined to mean a protonephridium and a metanephridium together. Hence, protonephromixia would have to be defined as ectodermal (or ectomesodermal) structures.

Another general issue concerning Goodrich's (1945) terminology is whether the various organs grouped as metanephromixia or mixonephridia are homologous. Smith (1988) clearly supported the idea that segmental organs have an ectodermal and mesodermal component in terebellids but regarded Goodrich's terminology as an oversimplification. The *A/Pwr* and *Mr* trees (Figs 67, 70, 71) suggest that the mixonephridia of terebellimorphs are homologous with the mixonephridia of groups such as sabellids and cirratulids, and in fact, this form of segmental organ is plesiomorphic for the Polychaeta. However, the results also suggest that the mixonephridia of scale worms could have been derived independently from other mixonephridia (ambiguous transformation series and not shown here). Spiomorph taxa (Spionidae, Apistobranchidae, etc.) were coded with '?' for mixonephridia and metanephromixia because there is no developmental evidence available, and Goodrich (1945) was uncertain about their classification. The results also suggest that mixonephridia is the appropriate classification for these polychaetes, but further investigation is needed. Metanephromixia are restricted to only a few polychaete families; Chrysopetalidae (questionably; see Appendix IV), Hesionidae, Ichthyotomidae and Syllidae. Investigation of the Sphaerodoridae and Pilargidae would be of interest, particularly in terms of the evolution of protonephromixia (see below).

What seems to be most required in the study of polychaete internal anatomy is more detailed studies of 'mixonephridia' in terms of both development and distributional patterns (see Smith 1988). The doubts raised by Bartolomaeus (1989) as to the accuracy of Goodrich's observations need to be assessed. Goodrich's (1945) terminology should be viewed as an initial attempt to outline homology hypotheses, further study is clearly required and changes will no doubt have to be made. Smith (1988) may well be right in arguing that Goodrich's terminology is too simplified.

Evolution of nephridia and segmental organs. While Goodrich (1945) regarded protonephridia as primitive for the Metazoa, he expressed no opinion as to the status of these structures in the Polychaeta, though he had previously (Goodrich 1900) considered them to be primitive. This change was presumably to allow for his theory that the separate metanephridia and coelomoducts found in the Clitellata and many capitellids represented the primitive annelid condition. The present results suggest that there is no evidence to support Goodrich's (1945) theory, and the separate nature of the gonoducts and nephridia in these two taxa is via convergence. In fact, the *A/Pwc* analysis shows separate coelomoducts and nephridia arising at least five times: in the Clitellata, Capitellidae, Myzostomidae, Nereididae, Protodrilidae and possibly Histriobdellidae (see Appendix IV).

Bartolomaeus (1989: 31) stated that "paired segmental protonephridia, which form a ciliated funnel of the proliferation of duct cells during maturity, belong to the ground pattern of annelids." His argument is based on the supposition that all polychaete metanephridial systems are completely ectodermal, whereas in non-polychaetes, phoronids are the provided example, and there is a mesodermal component to the metanephridia. Hence polychaete metanephridia cannot be homologous with any other metanephridial systems that do have a mesodermal component and so probably evolved secondarily from protonephridia (Bartolomaeus 1989: 31). Further data are clearly needed to provide support to Bartolomaeus's argument, particularly from within the Polychaeta and groups such as the Sipuncula and Echiura. As discussed above, there is evidence for a mesodermal component in the segmental organs of polychaetes.

Also, the results from this study (Figs 69, 72) suggest that the presence of protonephridia, with or without a funnel derived from the duct, is a secondary feature within the Polychaeta and cannot be considered plesiomorphic. The protonephridia present in phyllodocids and closely related taxa are not homologous with protonephridial systems in other polychaete taxa and hence cannot be considered as indicative of the plesiomorphic condition for the Polychaeta. Instead, the presence of protonephridia would appear to be the retention of some early developmental stage, and the appearance of the funnel is the final maturation of the metanephridium seen in polychaetes such as nereidids.

Such a conclusion is supported by data from other sources. Wilson & Webster (1974) reviewed the morphology of protonephridia in the Metazoa and found that considerable variation in form was classified under the term. They suggested that protonephridia had originated convergently a number of times. Westheide (1986) has provided additional evidence for such a conclusion within the Polychaeta. He argued that hesionids with adult protonephridia were derived from ancestors with a metanephridial condition. He then questioned the homology of all structures termed protonephridia in the Polychaeta. Unfortunately, an adequate phylogeny is not

available for the Hesionidae, and their monophyly has yet to be demonstrated, but the character coding used here followed Westheide's (1986) assumption that metanephridia are plesiomorphic for the group (see Appendix IV). While the trees in this study agree with Westheide's (1986) proposition that protonephridia can be derived from a metanephridial condition (Figs 69, 72), the cladistic proximity of the Hesionidae to the clade having adult protonephridia (nephtyids, glycerids etc.), and the lack of an adequate cladistic analysis for the group, suggests that the protonephridia of hesionids such as *Hesionides* and *Microphthalmus* should not necessarily be viewed as being independently derived. In other words, the derived position of *Hesionides* and *Microphthalmus* with reference to hesionids with metanephridia is, as yet, not proven.

Nephridia and circulation. Ruppert & Smith (1988) proposed a 'functional' model to explain the diversity of nephridial and circulatory systems in the Metazoa. Their model is based on the premise, that in bilaterally symmetrical animals, there are two fluid-filled compartments that are separated by a filter. When a blood vascular system (BVS) is present, it lies inside a coelomic cavity. Filtration units (podocytes) lie between the BVS and the coelom, and increased pressure in the BVS results in filtered vascular fluid entering the coelom. Reabsorption occurs via open ducts, and this system is termed 'metanephridial'. Thus, when a BVS is absent, there is no possibility for the 'metanephridial' system, as defined by Smith & Ruppert (1988), to exist, and so protonephridia have to be present.

Ruppert & Smith (1988: 252) suggest that there is a nearly perfect correlation between animals with blood vessels and metanephridia, and animals without blood vessels and protonephridia. While they did not perform any statistical tests to demonstrate that this was in fact the case, Smith & Ruppert (1988: 232) state that "The Polychaeta is an excellent group with which to test the predictions of our model". They also argue that "protonephridia and metanephridia are functionally adaptive to specific body plans occurring within the Polychaeta" (Smith & Ruppert 1988: 261). The data and results presented in this paper allow for a further assessment of their hypotheses. The available data for all polychaete families on the occurrence of adult nephridial forms and circulatory systems can be subjected to statistical tests treating all taxa as independent and also with allowance made for phylogenetic relationships implied by the cladograms presented here. The issues concerning the non-independence of data across clades are outlined in Harvey & Pagel (1991). The method used here for assessing Ruppert and Smith's (1988) hypothesis is derived from Ridley (1983). Additional examples can be found in Högland (1989) and Ridley (1986). This method assumes nothing about the directionality of the changes and only seeks to assess whether the perceived pattern of association can be regarded as significant.

Examination of the data matrices in Appendix II shows that 13 taxa are coded with adult protonephridia, 59 with metanephridia and 17 as unknown. The data matrices also show that 15 taxa are listed as having no BVS or a limited one. This is largely in agreement with Smith & Ruppert (1988: 234) and Ruppert & Smith (1988). However, the

Table 1. *Data for the occurrence of nephridial type and circulatory system based on information available in Appendix II. Terminal taxa are treated as independent variables (p < 0.001, Fischer's exact test)*

	BVS absent	BVS present	Total
Protonephridia	12	3	15
Metanephridia	5	47	52
Total	17	50	67

Table II. *Data for the occurrence of nephridial type and circulatory system based on information available in Appendix II. Data are now also based on the cladistic information shown in Fig. 65 and so allowing for phylogenetic effects (p = 0.3427, Fischer's exact test)*

	BVS absent	BVS present	Total
Protonephridia	4	3	7
Metanephridia	5	1	6
Total	9	4	13

Protodrilidae were coded as having a closed circulatory system based on Pierantoni (1908) rather than based on the observations for one species quoted by Smith & Ruppert (1988: 234). There are 57 taxa with a closed circulation (or an ostiate heart system), and 17 taxa are coded as unknown. Smith & Ruppert (1988) listed members of two taxa as having adult protonephridia that were coded here (Appendix II and Appendix IV) as (plesiomorphically) having metanephridia, the Hesionidae and Dorvilleidae (including Dinophilidae). Based on the analysis of Eibye-Jacobsen & Kristensen (1994), the species mentioned that now belong to the Dorvilleidae have independently acquired adult protonephridia (and lost a BVS). Based on the topology of trees shown here, the protonephridia (and lost BVS) found in some hesionids are also treated as being independently derived.

When the taxa from the matrices in Appendix II are treated as independent, and the Dorvilleidae and Hesionidae are each divided into two taxa, one with metanephridia and a BVS and another with protonephridia and no BVS, the 2 × 2 table shown in Table I is derived. The table also treats the Siboglinidae as two taxa based on the presence of protonephridia in some taxa (see Appendix IV sections on Frenulata and Vestimentifera). The 20 taxa for which information about either (or both) the nephridial system or circulatory system is lacking were excluded. Also, the Onychophora and Euarthropoda were excluded. This meant that 67 taxa could be considered (Table 1). For this table, the proportion of taxa having protonephridia with a limited BVS (0.18) is greater than those having metanephridia with a limited BVS (0.075, $p < 0.001$, Fischer's exact test). Thus, the current data available for the Polychaeta suggest that the model of Ruppert & Smith (1988) is supported. However, when phylogenetic effects are taken into consideration based on the cladogram shown in Fig. 65, which is essential for any such tests (see Ridley 1983; Harvey & Pagel 1991), there are only four independent occurrences of protonephridia with a limited or absent BVS and only one instance of metanephridia and a well-developed BVS (Table II). Under these circumstances, the co-occurrence of protonephridia with no/limited BVS (0.31) is not greater than that of metanephridia and no/limited BVS (0.38, $p = 0.3427$, Fischer's exact test).

On the evidence available for the taxa considered in this analysis, the data based on cladistic relationships do not support Ruppert and Smith's model. The problem with Ruppert and Smith's (1988) idea that there is strong support for their hypothesis lies in perceiving the Linnaean system as providing some sort of hierarchical level at which valid comparisons can be made. This is clearly not the case, and similar errors by other workers have resulted in calls for the abandonment of the Linnaean system (e.g. Sundberg & Pleijel 1994). To properly test models like the one proposed by Ruppert & Smith (1988), independent evolutionary events, based on phylogenetic hypotheses, are needed. These can only be discovered with confidence using cladistic techniques. Many more independent examples of the co-occurrence of protonephridia and the limitation or lack of a BVS are needed before their model can be interpreted as having any heuristic value.

The most interesting aspects of the Ruppert & Smith (1988) model are, of course, the exceptions. Of relevance to this paper, they are:

1. Taxa with metanephridial systems and no (or limited) circulatory system: Sipuncula, Ichthyotomidae, Capitellidae, Psammodrilidae and Sphaerodoridae.

2. Taxa with adult protonephridial systems and a well-developed circulatory system: the Siboglinidae (in part), Nephtyidae and Protodrilidae.

For taxa with metanephridia and no BVS, the site of 'primary' filtration becomes the problem of major interest. For the Sipuncula, Ruppert & Smith (1988: 25) cited evidence for the existence of podocytes on the compensation sacs that could serve the purpose of primary filtration. For the four polychaete taxa mentioned, further investigation is clearly required.

Of the taxa with protonephridia and a well-developed BVS, Ruppert & Smith (1988) and Smith & Ruppert (1988) explain that in the case of the Nephtyidae, this may be an adaptation to retain haemoglobin molecules present in the coelom. The A/Per and A/Pwr trees show that the Nephtyidae are the plesiomorphic group in a clade that can be identified by the presence of protonephridia. This implies that a circulatory system was lost after protonephridia were acquired in this clade (e.g. Fig. 69). Rather than seeking an adaptive explanation for the combination of protonephridia and a BVS in nephtyids, further study on the relationships among taxa with secondarily derived protonephridia may be more fruitful.

literature were used in several ways, which gave some different results. Clearly, further theoretical and computational advances in dealing with data sets is required that could not be addressed in this paper. However, the A/P method (Pleijel 1995) of coding (Appendix I and Appendix II) is one in which the maximum information in terms of initial homology hypotheses is preserved, and this may serve as an important database for future analyses.

The most significant results of this study are that:

1. The phylum Pogonophora should be incorporated into the Polychaeta and reduced in rank to that of family, the Siboglinidae in the clade Sabellida. Clearly, a major revision of the taxonomy within the Siboglinidae is now required.

2. The Articulata is supported by essentially the same apomorphies as identified by Rouse & Fauchald (1995) with the Echiura as sister group. Chaetae have either evolved twice, once in the Echiura and once in the Annelida, or the presence of such structures is plesiomorphic for the Articulata and they have been lost in the Arthropoda. The branch support for the Articulata (and Annelida) is weak, and a further investigation into the position of the Echiura should be pursued using molecular sequence data.

3. A traditionally formulated Annelida is monophyletic (though weakly supported) and, for the time being, is accepted as a valid taxon. It comprises two clades, the Clitellata and Polychaeta, though the monophyly of the latter is not well supported. The possibility that the Clitellata has a sister group amongst the polychaetes may have to be resolved on molecular sequence data.

4. The Aeolosomatidae and Potamodrilidae, formerly either members of the Clitellata or Annelida outside both the Polychaeta and Clitellata, now should be regarded as polychaetes. The status of the Myzostomidae now should be considered in relation to other taxa with a hypertrophied axial pharynx.

The new classification provided here is based on a somewhat arbitrary choice of tree, but it represents an improvement over those that are currently available. The use of Linnaean categories is avoided, and a hierarchical set of names is provided to group the 83 families that now should be regarded as polychaetes. If this paper succeeds in any way, it should be to show the level of knowledge that is minimally necessary before any drastic step, such as erecting a new family, is contemplated.

Conclusions

This study represents the first attempt to analyze currently available morphological data on polychaetes in a synthetic manner. Previous attempts at polychaete classification (reviewed in Fauchald & Rouse 1997) have been based on one or two organ systems at most. While the analyses presented here suffer from the flaws of incomplete knowledge about taxa (note the number of '?' in the matrices in Appendix Ia and Appendix IIb) and problems with coding of data (see section Methods), they arguably represent a considerable advance in polychaete systematics.

The data obtained from an extensive review of the

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Appendix I

a. Characters: Absence/presence coding based on Pleijel (1995)

In Appendix IIa, an affirmative for the statement is scored with a 1; a negative is scored with a 0. Unknown with '?'. No allowance is made for inapplicable states.

1. Prostomium clearly demarked by a distinct groove.
2. Prostomium fused to the peristomium, but distinct.
3. Prostomium fused to the peristomium, and limited.
4. Prostomium on peristomium, frontal edge fused.
5. Peristomium forms a distinct ring.
6. Peristomium forms two distinct rings.
7. Peristomium elongate.
8. Peristomium forms rings and a collar.
9. Peristomium limited to lips only.
10. Prostomial antennae.
11. Median prostomial antenna.
12. Pair of prostomial antennae.
13. Palps.
14. Grooved palps.
15. Prostomial grooved palps.
16. Peristomial grooved palps.
17. Prostomial paired palps.
18. Prostomial multiple palps.
19. Prostomial palps form a crown.
20. Peristomial paired palps.
21. Peristomial palps multiple.
22. Prostomial (sensory) palps.
23. Prostomial (sensory) palps ventral.
24. Prostomial (sensory) palps ventro-lateral.
25. Nuchal organs.
26. Nuchal organs as pits or grooves.
27. Nuchal organs form posterior projections.
28. Nuchal organ as caruncle.
29. Four or five longitudinal muscle bands.
30. Segmentation.
31. 1st segment indistinct.
32. 1st segment similar to those following.
33. 1st segment surrounds head.
34. 1st segment fused to head.
35. 1st segment dorso-lateral around head.
36. 1st segment elongate.
37. 1st segment appendages same as following.
38. 1st segment appendages/chaetae absent.
39. 1st segment tentacular cirri only.
40. 1st segment with notopodia only.
41. 1st segment with neuropodia only.
42. 1st segment with arthropod appendages.
43. Tentacular cirri.
44. Parapodia.
45. Parapodia with similar rami.
46. Parapodia with projecting neuropodia.
47. Parapodia in part with tori.
48. Parapodia in part notopodial ridges.
49. Parapodia spiomorph.
50. Dorsal cirri.
51. Dorsal cirri cirriform.
52. Dorsal cirri include elytra.
53. Dorsal cirri foliaceous.
54. Dorsal cirri limited.
55. Ventral cirri.
56. Parapodial branchiae.
57. Dorsal simple branchiae.
58. Dorsal flattened branchiae.
59. Dorsal branchiae in a few anterior chaetigers.
60. Lateral organs.
61. Dorsal cirrus organs.
62. Dorsal organs.
63. Epidermal papillae.
64. Pygidial cirri, One pair.
65. Pygidial cirri, Two or more pairs.
66. Dorsolateral folds.
67. No buccal organ.
68. Stomodaeum, axial, hypertrophied.
69. Stomodaeum, ventral buccal bulb.
70. Stomodaeum, disappears.
71. Stomodaeum, ventral hypertrophied.
72. Stomodaeum, axial simple.
73. Axial hypertrophied stomodaeum with jaws.
74. Axial hypertrophied stomodaeum one lateral pair of jaws.
75. Axial hypertrophied stomodaeum one or two D-V pairs of jaws.
76. Axial hypertrophied stomodaeum jaws form a cross or circle.
77. Proventricle.
78. Ventral buccal bulb not eversible.
79. Ventral buccal bulb eversible.
80. Ventral hypertrophied stomodaeum ridged.
81. Ventral hypertrophied stomodaeum with jaws.
82. Ventral hypertrophied stomodaeum jaws prionognath.
83. Ventral hypertrophied stomodaeum jaws labidognath.
84. Gular membrane.
85. Gut with lateral folds.
86. Gut with side branches.
87. Gut occluded.
88. Gut with a straight tube.
89. Adult metanephridia.
90. Adult protonephridia.
91. Ciliophagocytal organ.
92. Mixonephridia.
93. Metanephromixia.
94. Protonephromixia.
95. Coelomoducts and nephridia separate.
96. Nephridia and coelomoducts in most segments.
97. One pair of anterior excretory nephridia; posterior gonoducts.
98. Segmental organs restricted to a few middle segments.
99. Anterior sterile nephridia and posterior gonoducts.
100. Sperm with mitochondrial interpolation.
101. Circulatory system limited or absent.
102. Closed circulation.
103. Ostiate heart.
104. Heart body.
105. Chaetae.
106. Calcareous chaetae.
107. Chaetal inversion.
108. Aciculae.
109. Compound chaetae.
110. Compound chaetae with two ligaments.
111. Compound chaetae with one ligament.
112. Compound chaetae with a fold.
113. Compound chaetae taper.
114. Compound chaetae falcate.
115. Compound chaetae dentate.
116. Compound chaetae hooked.
117. Capillary chaetae.
118. Spines in one anterior chaetiger.
119. Spines generally.
120. Hooded chaetae.
121. Falcate hooks.
122. Dentate hooks.
123. Uncini.
124. Fine silk notochaetae.

b. Characters: Multistate coding

In Appendix IIb, scores that are unknown are indicated with '?' and non-applicable states with a '—'.

1. Prostomium; 0. Tentacles; 1. Flattened; 2. Acron; 3. Absent; 4. Distinct; 5. Fused, distinct groove; 6. Fused to the peristomium, limited but distinct; 7. Fused to the peristomium, frontal edge
2. Peristomium; 0. Sipunculid; 1. Acron; 2. Absent; 3. Ring; 4. Two rings; 5. Elongate; 6. Rings and collar; 7. Lips only
3. Prostomial antennae; 0. Absent; 1. Present
4. Prostomial antennae; 0. Median; 1. Lateral; 2. Median and Lateral
5. Palps; 0. Absent; 1. Present
6. Palps; 0. Grooved; 1. Ventral Sensory
7. Grooved palps; 0. Prostomial; 1. Peristomial
8. Prostomial grooved palps; 0. Prostomial pair; 1. Prostomial multiple; 2. Prostomial crown
9. Peristomial grooved palps; 0. Peristomial pair; 1. Peristomial papillated; 2. Peristomial multiple
10. Ventral sensory palps position; 0. Ventral; 1. Ventro-lateral
11. Nuchal organs; 0. Absent; 1. Pits or grooves; 2. Posterior projections; 3. Caruncle
12. Longitudinal muscle bands; 0. Absent; 1. Present
13. Segmentation; 0. Absent; 1. Present
14. First segment; structure; 0. Indistinct; 1. Similar; 2. Surround head; 3. Fused to head; 4. Dorso-lateral around head; 5. Elongate; 6. Arthropod
15. First segment; appendages; 0. Same as following; 1. Absent; 2. Tentacular cirri only; 3. Notopodia only; 4. Neuropodia only; 5. Arthropod; 6. Frenulate
16. Tentacular cirri; 0. Absent; 1. Present

17. Parapodia; 0. Absent; 1. Rami similar; 2. Neuropodia larger; 3. Tori present; 4. Notopodial ridges; 5. Spiomorph; 6. Uniramous (saccocirrid)
18. Dorsal cirri; 0. Absent; 1. Cirriform; 2. Elytra (plus cirri in some); 3. Foliaceous; 4. Limited; 5. Narrow, elongate
19. Ventral cirri; 0. Absent; 1. Present
20. Gills; 0. Absent; 1. Parapodial; 2. Dorsal simple; 3. Dorsal flat; 4. Dorsal in a few anterior chaetigers; 5. Interramal; 6. Single
21. Lateral organs; 0. Absent; 1. Present
22. Dorsal cirrus organ; 0. Absent; 1. Present
23. Dorsal organs; 0. Absent; 1. Present
24. Epidermal papillae; 0. Absent; 1. Present
25. Pygidial cirri; 0. Absent; 1. Present (one pair); 2. Present (more than one pair).
26. Dorso-lateral folds; 0. Absent; 1. Present
27. Stomodaeum; 0. Sipunculid; 1. Echiurid; 2. Arthropod; 3. Absent; 4. Dorsally muscularised; 5. No buccal organ; 6. Axially hypertrophied; 7. Ventral buccal organ; 8. Ventrally hypertrophied; 9. Axial simple; A. Cossurid; B. Psammodrilid; C. Spintherid
28. Axial jaws; 0. Absent; 1. Lateral pair; 2. 'D-V pairs'; 3. Cross or circle; 4. Single tooth
29. Proventricle; 0. Absent; 1. Present
30. Ventral buccal organ; 0. Eversible; 1. Non-eversible
31. Ventral hypertrophied pharynx; armature; 0. Ridged; 1. Jaws
32. Ventral hypertrophied pharynx; jaws; 0. Ctenognath; 1. Prionognath; 2. Labidognath
33. Gular membrane; 0. Absent; 1. Present
34. Gut; 0. Sipunculid; 1. Echiurid; 2. Straight; 3. Lateral folds; 4. Side branches; 5. Occluded
35. Nephridia; 0. Metanephridia; 1. Protonephridia
36. Ciliophagocytal organ; 0. Absent; 1. Present
37. Metanephridial elaboration; 0. None; 1. Mixonephridia; 2. Metanephromixia
38. Protonephridial elaboration; 0. None; 1. Protonephromixia
39. Distribution of segmental organs; 0. Not segmental; 1. Along body; 2. Anterior excretory pair of nephridia posterior gonoducts; 3. Restricted; 4. Anterior sterile; posterior gonoducts; 5. Arthropod; 6. Clitellate; 7. Capitellid; 8. Histriobdellid; 9. Oweniid; A. Myzostome; B. Questid
40. Sperm mitochondria; 0. Not interpolated between nucleus and axoneme; 1. Interpolated between nucleus and axoneme
41. Circulation; 0. Absent/limited; 1. Closed; 2. Ostiate heart with haemocoel
42. Heart body; 0. Absent; 1. Present
43. Chaetae; 0. Absent; 1. Present
44. Chaetal composition; 0. Chitinous; 1. Calcareous
45. Chaetal inversion; 0. Absent; 1. Present
46. Aciculae; 0. Absent; 1. Present
47. Compound chaetae; 0. Absent; 1. Single ligament; 2. Double ligament; 3. Fold
48. Compound shape; 0. Tapers; 1. Falcate; 2. Dentate; 3. Hooked
49. Capillary chaetae; 0. Absent; 1. Present
50. Spines in one anterior chaetiger; 0. Absent; 1. Present
51. Spines; 0. Absent; 1. Present
52. Hooded chaetae; 0. Absent; 1. Present
53. Hooks; 0. Absent; 1. Falcate; 2. Dentate
54. Uncini; 0. Absent; 1. Present
55. Silky chaetae; 0. Absent; 1. Present

Appendix II

a. Matrix of A/P coding scores used in both A/Pe and A/Pw analyses. Present is coded with '1'. Unknown is coded with '?'.

Taxon	Coding (characters 1–135)
Sipuncula	000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Echiura	000000010000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Enarthropoda	000000000000000000000000010000000000001000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Onychophora	000000000000000000000000010000000000001000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Clitellata	100010000000000000000000011010001000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Frenulata	100001000011010001000??00110000100000010010000000000000000000000000000000000000000000000000000000
Vestimentifera	001000100001101000100??00110001000010000001010000000000010000000000100??0010
Aberrantidae	100010001101000000001011100110010000000011010001110010000000000010
Acoetidae	100000011110000000011001100100010000100001101000111001000000000010
Acrocirridae	100000010001101000100011100?101000001000011000000000001000?00100
Aeolosomatidae	010000000000000000000110010100010000010000001001000000000010
Alciopidae	100000111100000011011100?110000100011010001001010000000?00000
Alvinellidae	100000010001101000100011001100010000010000000110000100001
Ampharetidae	100000010001010001001100110001000000110001100011000000000
Amphinomidae	100000111100000101100111000101000001101000111001000000010
Aphroditidae	100000111010000011011001100100010000011010001110010000001
Apistobranchidae	100000010011010001000101101000010000010011000001010000000001
Arenicolidae	100000010000000000001100110100010000100100000000000
Capitellidae	100000010000000000001100110100010000100100000000000
Chaetopteridae	100000010011010001000101101000000010011000110001000000010
Chrysopetalidae	100000111100001101100?10010000010000110000001000000
Cirratulidae	100000010011010001000110011010000100000110000000
Cossuridae	100100000000000000001100010100010000000010000001
Ctenodrilidae	100000100000000000001100110100010000000000010
Diurodrilidae	100100000000000000??00?1010000000000010001001000010
Dorvilleidae	100010001110000010111001101000100011010011001000010
Eulepethidae	100000111100000011011100?100100010001101000110001000010
Eunicidae	100010001110000010111001101000010001011000110001000010
Euphrosinidae	100000111100000010?1001110001010000010000110?00100
Fauveliopsidae	100000100011010001000110?10100010000010000100?00100
Flabelligeridae	100000010011010001000110011000010000100000000?00100
Glyceridae	100000110110000000011000011010000100010001001000010
Goniadidae	100000110110000011000011010000011000101001??0010
Hartmaniellidae	100000100000001001100?101000010001101000110001000010
Hesionidae	100000111100000011011001110000001001101000110001000?0000
Histriobdellidae	100100001111000000101??001101000000011010001100010?0000
Iospilidae	100000100000000011011001?110000010001101000100??0010
Ichthyotomidae	010000111100000011011001101000001101000110010101
Lacydoniidae	100000110110000011011001110000010000100000100?0000
Longosomatidae	100000100011000100001010?10100010000100000010?0?10
Lopadorhynchidae	100000110110000011011100?1100001011000101010?0?10
Lumbrineridae	100010001110000000011001101000010001000110000100010
Magelonidae	100000100011000000000011001101000010001000000001
Maldanidae	010000100000000000110011010001000010001100100000
Myzostomidae	001000010000000??00?1010000010001100010000000
Nautiliniellidae	010000110110000011?0??00?1010000011100011001000010
Nephtyidae	100000101100000011011001110000011000110001000010
Nereididae	100000110110000011011001101000010001100000000010
Nerillidae	010000111100000101110001010001001000100010010
Oenonidae	100010001110000010111001101000010001100110001000010
Onuphidae	100100001111000010111001101000010000100010001
Opheliidae	100000100000000001100110100010000110000101001001
Orbiniidae	100100000000000001100110100010001001000000000
Oweniidae	001010000111010000??001101000010001100100000???
Paralacydoniidae	100000110110000011??00?1100000001001100000010100001
Paraonidae	010000111100000001100110100010001000000000
Parergodrilidae	010010000000000001100110100010000000011000
Pectinariidae	001000010001101000100011001101000101001000010
Pholoidae	100000111100000011011100??00?100100010001101000100100010
Phyllodocidae	100000111100000110110011100000100110100011001000010
Pilargidae	100000111100000110110011100000100110100011001000010
Pisionidae	100000111011000000110001110001000010000100001
Poecilochaetidae	100000100011010001010110100001000100000100000100
Poeobiidae	100000100011010001000110?101000000000000100000
Polygordiidae	010010000011010000011001101000010001101100000010
Polynoidae	100000111100000011011001100100010001101000110001000010
Pontodoridae	100000110110000011011100?110000100011010001100010000
Potamodrilidae	010000100000000001100110100010000000010
Protodrilidae	010010000111010000011001101000010000000000
Protodriloididae	010010000111010000011001101000010000000000
Psammodrilidae	100000000000000001100?101000010000110000000100100001
Questidae	100100000000000001100?101000010000110000000
Sabellariidae	001000010001101000100011001100010001001010000
Sabellidae	001000010000111001000011001101000010000010
Saccocirridae	100100000111010000011001101000010000100000010001000001
Scalibregmatidae	100100000000000001100110100010001001000001
Serpulidae	001000010000111001000011001101000010000010
Sigalionidae	100000111100000110110011001000010001101000111001000010
Sphaerodoridae	100000111100000110110011001001000010000100000010
Spintheridae	100000111000000000?100101001000101000000100001
Spionidae	100000111011010001000101011010000100000010101001
Sternaspidae	100000010000000??00001010000100010000100100
Syllidae	100000111100000110110011001000110001000001000000
Terebellidae	001000010001110010000011001100010001001000000000
Tomopteridae	010000010001000000110?1100?11000001001101000000
Trichobranchidae	000100001000110000000?100?11000001001101000000
Trochochaetidae	100000011011010001000100101011010001000010010001
Typhloscolecidae	100000111100000001100111000010001101000100101000010
Uncispionidae	100000111011010001000??00?1010000100001000000010?00001

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b. Matrix of multistate coding scores used in both Mr *and* Mc *analyses.* The OR separator '/' is used when some of the possible states in the character could be eliminated. Unknown is coded with '?' and non-applicable with '—'.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Sipuncula	0	0	0	-	0	-	-	-	-	-	0	0	0	-	-	-	0	-	-	0	0	-	0	0	-	0	0	-
Echiura	1	7	0	-	0	-	-	-	-	-	0	0	0	-	-	-	0	-	-	0	0	-	0	0	-	0	1	-
Euarthropoda	2	1	0	-	0	-	-	-	-	-	0	1	1	6	6	-	0	-	-	0	0	-	0	0	0	0	2	-
Onychophora	3	2	-	-	-	-	-	-	-	-	0	1	1	6	6	-	0	-	-	0	0	-	0	0	0	1	3	-
Clitellata	4	3	0	-	0	-	-	-	-	-	0	1	1	1	0	-	0	-	-	0	0	-	0	0	0	0	7	-
Frenulata	4	5	0	-	1	0	1	-	0	-	0/1	1	1	5	5	0	3	0	0	0	0	-	0	0	0	0	7	-
Vestimentifera	6	5	0	-	1	0	1	-	2	-	0/1	1	1	5	1	0	3	0	0	0	0	-	0	0	0	0	7	-
Aberrantidae	4	4	1	0	1	1	-	-	-	1	1	1	1	1	0	0	2	0	0	2	?	-	0	0	1	?	6/8/9	-
Acoetidae	4	7	1	2	1	1	-	-	-	0	1	1	1	2	0	1	2	2	1	0	0	0	0	0	1	0	5	2
Acrocirridae	4	7	0	-	1	0	1	-	0	-	1	?	1	1	1	0	1	0	0	2	?	-	0	1	0	?	6	-
Aeolosomatidae	5	7	0	-	0	-	-	-	-	-	1	0	1	1	0	-	0	-	-	0	0	-	0	0	0	0	6	-
Alciopidae	4	7	1	2	1	1	-	-	-	0	1	?	1	0	2	1	2	3	1	0	0	0	0	0	1	0	5	0
Alvinellidae	4	7	0	-	1	0	1	-	2	-	1	1	1	3	1	0	3	0	0	4	?	-	0	0	0	0	6	-
Ampharetidae	4	7	0	-	1	0	1	-	2	-	1	1	1	3	1	0	3	0	0	4	1	-	0	0	2	0	6	-
Amphinomidae	4	7	1	2	1	1	-	-	-	1	3	1	1	4	0	0	1	1	1	1	0	0	0	0	0	1	8	-
Aphroditidae	4	7	1	0	1	1	-	-	-	0	1	1	1	2	0	1	2	2	1	0	0	0	0	0	1	0	5	2
Apistobranchidae	4	7	0	-	1	0	1	-	0	-	2	1	1	1	0	0	5	5	0	0	1	0	0	0	0	1	9	-
Arenicolidae	4	7	0	-	0	-	-	-	-	-	1	1	1	1	1	0	3	0	0	1	0	-	0	0	0	1	9	-
Capitellidae	4	7	0	-	0	-	-	-	-	-	1	1	1	1	1	0	3	0	0	0	1	-	0	0	0	1	9	-
Chaetopteridae	4	7	0	-	1	0	1	-	0	-	2	1	1	1	3	0	3	0	0	0	?	-	0	0	0	?	4	-
Chrysopetalidae	4	7	1	2	1	1	-	-	-	0	1	?	1	2	0	1	4	1	1	0	0	0	0	0	1	0	5	1
Cirratulidae	4	7	0	-	1	0	1	-	0	-	1	1	1	1	1	0	1	0	0	2	0	-	0	0	0	1	6	-
Cossuridae	4	3	0	-	0	-	-	-	-	-	1	1	1	1	0	0	1	0	0	6	0	-	0	0	2	0	A	-
Ctenodrilidae	4	7	0	-	0	-	-	-	-	-	1	0	1	1	1	-	0	-	-	2	0	-	0	0	0	1	6	-
Diurodrilidae	4	3	0	-	0	-	-	-	-	-	0/1	?	1	1	-	-	0	-	-	0	0	-	0	0	1	1	6	-
Dorvilleidae	4	4	1	2	1	1	-	-	-	1	1	1	1	1	0	0	2	1	1	0	0	1	0	0	1	1	8	-
Eulepethidae	4	7	1	2	1	1	-	-	-	0	1	?	1	2	0	1	2	2	1	0	0	0	0	0	1	0	5	2
Eunicidae	4	4	1	2	1	1	-	-	-	1	1	1	1	0	0	2	1	1	1	0	0	0	0	0	1	1	8	-
Euphrosinidae	4	7	1	2	?	?	?	?	?	?	3	1	1	4	0	0	4	1	1	1	0	0	0	0	1	1	6	-
Fauveliopsidae	4	7	0	-	1	0	1	-	0	-	1	?	1	1	0	0	1	0	0	0	?	-	0	1	0	1	6	-
Flabelligeridae	4	7	0	-	1	0	1	-	0	-	1	1	1	1	0	0	2	1	1	0	0	0	0	0	1	0	5	3
Glyceridae	4	7	1	1	1	1	-	-	-	0	0	1	1	1	4	0	2	1	1	0	0	0	0	0	1	0	5	3
Goniadidae	4	7	1	1	1	1	-	-	-	0	0	1	1	1	0	0	2	1	1	2	?	?	0	0	1	1	8	-
Hartmaniellidae	4	4	0	-	0	-	-	-	-	-	1	?	1	1	0	0	2	1	1	0	0	0	0	0	1	0	5	1
Hesionidae	4	7	1	2	1	1	-	-	-	0	1	1	1	0	2	1	2	1	1	0	0	0	0	0	1	0	5	1
Histriobdellidae	4	3	1	2	1	1	-	-	-	1	0/1	1	1	1	-	-	0	-	-	0	0	-	0	0	0	1	8	-
Ichthyotomidae	5	7	1	2	1	1	-	-	-	0	1	1	1	1	0	0	2	1	1	0	?	?	0	0	1	?	5	1
Iospilidae	4	7	0	-	1	1	-	-	-	0	1	?	1	0	2	1	2	1	1	0	0	?	0	0	0	0	5	1
Lacydoniidae	4	7	1	1	1	1	-	-	-	0	1	1	1	0	2	1	2	3	1	0	0	0	0	0	2	0	5	0
Longosomatidae	4	7	0	-	1	0	1	-	0	-	2	?	1	1	1	0	5	0	0	2	?	-	0	0	0	?	6	-
Lopadorhynchidae	4	7	1	1	1	1	-	-	-	0	1	?	1	0	2	1	2	3	1	0	?	?	0	?	0	0	5	0/1
Lumbrineridae	4	4	1	2	0	-	-	-	-	-	1	1	1	1	0	0	2	4	1	0	0	1	0	0	1	1	8	-
Magelonidae	4	7	0	-	1	0	1	-	1	-	0	1	1	1	1	0	5	0	0	0	1	-	0	0	0	1	6	-
Maldanidae	5	7	0	-	0	-	-	-	-	-	1	1	1	1	1	0	3	0	0	0	0	-	0	0	2	1	6/9	-
Myzostomidae	6	7	0	-	0	-	-	-	-	-	0/1	?	1	1	0	0	2	1	1	0	0	0	0	0	0	?	5	0
Nautiliniellidae	5	7	1	1	1	1	-	-	-	0	0/1	?	1	1	0	0	2	1	1	1	0	1	0	0	0	0	5	0
Nephtyidae	4	7	1	1	1	1	-	-	-	0	1	1	1	0	0	1	1	1	1	5	0	0	0	0	1	0	5	1
Nereididae	4	7	1	1	1	1	-	-	-	0	1	1	1	0	2	1	2	1	1	0	0	0	0	0	1	0	5	1
Nerillidae	5	7	1	2	1	1	-	-	-	1	1	1	1	0	0	1	0	0	0	0	0	-	0	0	1	1	6	-
Oenonidae	4	4	1	2	0	-	-	-	-	-	1	1	1	1	0	0	2	4	0	0	0	1	0	0	1	1	8	-
Onuphidae	4	3	1	2	1	1	-	-	-	1	1	1	1	0	0	2	1	1	1	0	1	0	1	0	0	1	8	-
Opheliidae	4	7	0	-	0	-	-	-	-	-	1	1	1	1	0	0	1	0	0	3	1	0	1	0	2	1	6	-
Orbiniidae	4	3	0	-	0	-	-	-	-	-	1	1	1	1	3	0	3	0	0	0	0	-	0	0	0	1	6	-
Oweniidae	6	3	0	-	1	0	0	0	-	-	0/1	1	1	1	3	0	3	0	0	0	0	0	0	0	?	0	5	0
Paralacydoniidae	4	7	1	1	1	1	-	-	-	0	0/1	?	1	0	4	0	2	1	1	0	0	0	0	0	2	1	6	-
Paraonidae	5	7	1	0	0	-	-	-	-	-	1	1	1	1	0	0	1	0	0	3	1	-	0	0	0	0	6	-
Parergodrilidae	5	3	0	-	0	-	-	-	-	-	1	1	1	1	0	-	0	-	-	0	0	-	0	0	0	1	6	-
Pectinariidae	6	7	0	-	1	0	1	-	2	-	1	1	1	3	3	0	3	0	0	4	1	-	0	0	0	1	6	-
Pholoidae	4	7	1	2	1	1	-	-	-	0	0/1	?	1	2	0	1	2	2	1	0	0	0	0	0	1	0	5	2
Phyllodocidae	4	7	1	2	1	1	-	-	-	0	1	1	1	0	2	1	2	3	1	0	0	0	0	0	1	0	5	0
Pilargidae	4	7	1	2	1	1	-	-	-	0	1	?	1	0	2	1	2	1	1	0	0	0	0	0	1	0	5	2
Pisionidae	4	7	1	1	1	1	-	-	-	0	0	1	1	1	0	0	2	1	1	0	0	0	0	0	1	0	6	-
Poecilochaetidae	4	7	0	-	1	0	1	-	0	-	2	1	1	1	0	0	5	0	0	1	1	-	0	0	2	1	6	-
Poeobiidae	4	7	0	-	1	0	1	-	0	-	1	?	1	1	1	-	0	-	-	2	0	-	0	1	0	1	6	-
Polynoidae	4	7	1	2	1	1	-	-	-	0	1	1	1	2	2	1	2	2	1	0	0	0	0	0	1	0	5	2
Polygordiidae	5	3	0	-	1	0	0	0	-	-	1	1	1	1	1	-	0	-	-	0	0	-	0	0	1	1	4	-
Pontodoridae	4	7	1	1	1	1	-	-	-	0	1	?	1	0	2	1	2	1	1	0	0	0	0	0	1	0	5	0
Potamodrilidae	5	7	0	-	0	-	-	-	-	-	1	1	1	1	0	0	0	-	-	0	0	-	0	0	0	1	6	-
Protodrilidae	5	3	0	-	1	0	0	0	-	-	1	1	1	1	0	-	0	-	-	0	0	-	0	0	1	1	6	-
Protodriloididae	5	3	0	-	1	0	0	0	-	-	1	1	1	1	0	-	0	-	-	0	0	-	0	0	1	1	6	-
Psammodrilidae	4	3	0	-	0	-	-	-	-	-	1	1	1	1	1	0	3	0	0	0	0	-	0	0	0	?	B	-
Questidae	4	3	0	-	0	-	-	-	-	-	1	?	1	1	0	0	1	0	0	2	1	-	0	0	2	1	6	-
Sabellariidae	6	7	0	-	1	0	1	-	0	-	1	1	1	3	3	0	3	0	0	3	0	-	0	0	0	0	4	-
Sabellidae	6	6	0	-	1	0	0	2	-	-	1	1	1	1	3	0	3	0	0	0	0	-	0	0	1	1	6	-
Saccocirridae	4	3	0	-	1	0	0	0	-	-	1	1	1	1	0	0	6	0	0	0	0	-	0	0	2	0	9	-
Scalibregmatidae	4	3	0	-	0	-	-	-	-	-	1	1	1	1	1	0	3	0	0	0	0	-	0	0	0	0	4	-
Serpulidae	6	6	0	-	1	0	0	2	-	-	1	1	1	1	3	0	3	0	0	0	0	-	0	0	1	1	6	-
Sigalionidae	4	7	1	2	1	1	-	-	-	0	1	1	1	2	0	1	2	2	1	0	0	0	0	0	1	0	5	2
Sphaerodoridae	4	7	1	2	1	1	-	-	-	0	1	1	1	0	2	1	2	0	0	0	0	-	0	0	1	0	5	0
Spintheridae	4	7	1	0	0	-	-	-	-	-	0	?	1	4	0	0	4	0	1	0	0	-	0	0	1	1	?	C
Spionidae	4	7	1	0	1	0	1	-	0	-	2	1	1	1	0	0	5	0	0	2	1	-	0	1	2	1	6/9	-
Sternaspidae	4	7	0	-	0	-	-	-	-	-	0/1	0	1	1	0	0	1	0	0	2	0	-	0	1	0	0	9	-
Syllidae	4	7	1	2	1	1	-	-	-	0	1	1	1	2	1	2	1	1	0	0	0	0	0	0	1	0	5	4
Terebellidae	7	7	0	-	1	0	0	1	-	-	1	1	1	3	1	0	3	0	0	4	0	-	0	0	0	1	6	-
Trichobranchidae	7	7	0	-	1	0	0	1	-	-	1	?	1	3	1	0	3	0	0	4	0	-	0	0	0	1	6	-
Trochochaetidae	4	7	1	0	1	0	1	-	0	-	2	1	1	1	0	0	5	0	0	0	1	-	1	0	2	0	9	-
Tomopteridae	5	7	0	-	1	1	-	-	-	0	1	?	1	0	2	1	2	0	0	0	0	-	0	0	0	0	5	0
Typhloscolecidae	4	7	1	0	0	-	-	-	-	-	1	1	1	0	2	1	2	3	1	0	0	0	0	0	1	0	5	0
Uncispionidae	4	7	1	0	1	0	1	-	0	-	0/1/2	?	1	1	0	0	5	0	0	3	?	-	0	0	2	?	9	-

29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
-	-	-	-	-	0	0	0	0	-	0	0	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	1	0	0	?	-	0	0	1	0	1	0	0	0	0	-	0	-	0	0	1	0	0
-	-	-	-	0	2	0	0	0	-	5	0	2	0	0	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	0	2	0	0	0	-	5	1	2	0	0	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	0	2	0	0	0	-	6	1	1	0	1	0	0	0	0	-	1	0	1	0	0	0	0
-	-	-	-	0	5	1	0	-	?	2	0	1	0	1	0	0	0	0	-	0	0	0	0	0	1	0
-	-	-	-	0	5	0	0	?	-	2	0	1	0	1	0	0	0	0	-	1	0	0	0	0	1	0
-	?	?	?	?	2	?	?	?	?	1/3/4	?	0/1	0	1	0	0	0	0	-	1	0	0	0	0	0	0
0	-	-	-	0	4	0	0	?	?	1/3/4	?	0/1	?	1	0	0	1	0	-	1	0	1	0	0	0	1
-	0	-	-	?	2	0	0	1	-	2	0	1	1	1	0	0	0	3	3	1	0	0	0	0	0	0
-	0	-	-	0	2	0	0	1	-	1	0	1	0	1	0	0	0	0	-	1	0	0	0	0	0	0
0	-	-	-	0	2	1	0	-	1	1	0	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0
-	1	-	-	1	3	0	0	1	-	3	1	1	?	1	0	0	0	0	-	1	1	0	0	0	1	0
-	1	-	-	1	3	0	0	1	-	3	0	1	1	1	0	0	0	0	-	1	1	0	0	0	1	0
-	-	0	-	0	2	0	0	1	-	1	0	1	0	1	1	0	1	0	-	1	0	1	0	0	0	0
0	-	-	-	0	4	0	0	1	-	1	?	1	0	1	0	0	1	0	-	1	0	1	0	0	0	1
-	-	-	-	0	2	0	0	1/2	-	4	0	1	0	1	0	0	0	0	-	1	0	0	0	0	0	0
-	-	-	-	1	2	0	0	1	-	3	0	1	0	1	0	0	0	0	-	1	0	0	0	2	0	0
-	-	-	-	1	2	0	0	0	-	7	0	0	-	1	0	0	0	0	-	1	0	0	1	2	0	0
-	-	-	-	0	2	0	0	1/2	-	4	0	1	0	1	0	0	0	0	-	1	1	0	0	0	1	0
0	-	-	-	0	2	0	0	2	-	1/3/4	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0
-	0	-	-	1	2	0	0	1	-	2	0	1	1	1	0	0	0	0	-	1	0	1	0	0	0	0
-	-	-	-	0	2	?	?	?	?	4	0	1	0	1	0	0	0	0	-	1	0	0	0	0	0	0
-	0	-	-	0	2	0	0	1	-	2	?	1	1	1	0	0	0	0	-	1	0	0	0	2	0	0
-	0	-	-	0	2	1	0	-	?	3/4	0	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-
-	-	1	0	0	2	0	0	1/2	-	1	0	1	0	1	0	0	1	2	2	1	0	0	0	0	0	0
0	-	-	-	0	4	0	?	?	?	1/3/4	?	0/1	?	1	0	0	1	0	-	1	0	1	0	0	0	0
-	-	1	1	0	2	0	0	1	-	1	0	1	0	1	0	0	1	2	2	1	0	0	1	0	0	0
-	-	0	-	0	2	0	0	1	-	1	?	1	0	1	1	0	1	0	-	1	0	1	0	0	0	0
-	0	-	-	1	2/3/4	?	?	?	?	1/2/3/.	?	1	?	1	0	0	0	0	-	1	0	0	0	0	0	0
-	0	-	-	1	3	0	0	1	-	2	0	1	1	1	0	0	0	3	3	1	0	0	0	0	0	0
0	-	-	-	0	2	1	1	-	1	1	?	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0
0	-	-	-	?	2/4	1	0	-	1	4	0	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0
-	-	1	2	?	2	?	?	?	?	1/3/4	?	0/1	?	1	0	0	1	2	0	1	0	0	0	0	0	0
0	-	-	-	0	2	0	1	2	-	1	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0
-	-	1	2	0	2	1	0	-	0	8	0	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-
0	-	-	-	0	2	0	0	2	-	1	0	0	-	1	0	0	1	1	0/2	1	0	0	0	0	0	0
0	-	-	-	?	2/4	?	?	?	?	1/3/4	?	0/1	?	1	0	0	1	1	0	0	0	0	0	0	0	0
0	-	-	-	0	2	?	?	?	?	1/3/4	?	0/1	?	1	0	0	1	1	0	1	0	0	0	0	0	0
-	0	-	-	?	2/4	?	?	?	?	1/3/4	?	0/1	?	1	0	0	0	0	-	1	0	1	0	0	0	0
0	-	-	-	?	2/4	?	?	?	?	1/3/4	?	0/1	?	1	0	0	1	1	0	0	0	0	0	0	0	0
-	-	1	1	0	2	0	0	1	-	1/3/4	0	0/1	?	1	0	0	1	2	2	1	0	0	0	0	0	0
-	0	-	-	0	2	?	?	?	?	4	0	1	0	1	0	0	0	0	-	1	0	0	1	2	0	0
-	?	-	-	1	2	0	0	1	-	3	0	1	0	1	0	0	0	0	-	1	0	0	0	2	0	0
0	-	-	-	0	4	1	0	-	0	A	0	0	-	1	0	0	1	0	-	1	0	0	0	1	0	0
1	-	-	-	?	2/4	?	?	?	?	1/3/4	?	0/1	?	1	0	0	1	0	-	1	0	0	0	0	0	0
0	-	-	-	0	2	1	1	-	1	1	?	1	0	1	0	0	1	0	-	1	0	0	0	0	0	0
0	-	-	-	0	2	0	1	2	-	1	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0
-	0	-	-	0	2	0	0	1	-	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0
-	-	1	2	?	2/4	?	?	?	?	1/3/4	?	1	0	1	0	0	1	0	-	1	0	0	0	0	0	0
-	-	1	1	0	2	0	0	1	-	1/4	0	1	0	1	0	0	1	2	2	1	0	0	0	0	0	0
-	-	-	-	1	2	0	0	1	-	1/3/4	0	1	1	1	0	0	0	0	-	1	0	0	0	0	0	0
-	0	-	-	0	2	0	0	1/2	-	1	?	1	?	1	0	0	0	0	-	1	0	1	0	0	0	0
-	0	-	-	0	2	0	0	1	-	9	0	1	0	1	0	0	0	0	-	1	0	0	0	2	0	0
0	-	-	-	?	2/4	?	?	?	?	1/3/4	?	0/1	?	1	0	0	1	1	0	1	0	0	0	0	0	0
-	0	-	-	0	2	0	0	1/2	-	4	0	1	0	1	0	0	0	0	-	1	0	0	1	0	0	0
-	0	-	-	0	2	0	0	?	?	1/3/4	?	1	-	1	0	0	0	0	-	1	0	0	0	0	0	0
-	1	-	-	1	3	0	0	1	-	3	0	1	1	1	0	0	0	0	-	1	1	0	0	0	1	0
0	-	-	-	0	2	0	?	1/2	-	4	0	0/1	?	1	0	0	1	1	2	1	0	0	0	0	0	0
0	-	-	-	0	2	1	0	-	1	1	0	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0
0	-	-	-	?	2/4	?	?	?	?	1/3/4	?	0/1	?	1	0	0	1	0	-	1	0	1	0	0	0	0
0	-	-	-	0	2	1	0	-	1	3	0	0	-	1	0	0	1	1	1	1	0	0	0	0	0	0
-	0	-	-	0	2	0	0	1/2	-	4	0	1	0	1	0	0	0	0	-	1	0	1	0	0	0	0
-	0	-	-	1	3	0	0	1	-	2	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-
0	-	-	-	0	4	0	0	1	-	1	0	1	0	1	0	0	1	0	-	1	0	1	0	0	0	0
-	-	-	-	0	2	0	0	-	-	1	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-
1	-	-	-	0	2	?	?	?	?	1/3/4	0	0/1	?	1	0	0	1	1	0	0	0	0	0	0	0	0
-	0	-	-	0	2	0	0	?	-	3	0	1	0	1	0	0	0	0	-	1	0	0	0	0	0	0
-	0	-	-	0	2	1	0	2	0	3	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-
-	0	-	-	0	2	0	0	?	-	4	0	1	0	1	0	0	0	0	-	0	0	0	0	2	0	0
-	-	-	-	0	2	0	0	?	-	4	0	0	-	1	0	0	0	0	-	0	0	0	0	2	0	0
-	0	-	-	0	2	?	0	?	?	B	0	1	0	1	0	0	0	0	-	1	0	0	0	2	0	0
-	-	-	-	0	2	0	0	1	-	2	0	1	1	1	0	1	0	0	-	1	1	0	0	0	1	0
-	-	-	-	0	2	0	0	1	-	2	0	1	0	1	0	1	0	0	-	1	0	0	0	2	1	0
-	0	-	-	0	2	0	0	?	-	1	?	1	0	1	0	0	0	0	-	1	0	0	0	0	0	0
-	-	-	-	0	2	0	0	1	-	1	?	1	0	1	0	0	0	0	-	1	0	0	0	0	0	0
-	-	-	-	0	2	0	0	1	-	2	0	1	0	1	0	1	0	0	-	1	0	0	0	0	1	0
0	-	-	-	0	4	0	0	1	-	1	0	1	0	1	0	0	1	1	2	1	0	0	0	0	0	0
1	-	-	-	0	2	0	0	1/2	-	3	?	0	-	1	0	0	1	1	1	1	0	0	0	0	0	0
-	-	-	-	0	4	?	?	?	?	1/3/4	?	1	0	1	0	0	1	3	3	0	0	1	0	0	0	0
-	?	-	-	0	2	0	0	1/2	-	4	0	1	0	1	0	0	0	0	-	1	0	0	1	2	0	0
-	-	-	-	0	3	0	0	1	-	2	?	1	0	1	0	0	0	0	-	1	1	0	0	0	0	0
1	-	-	-	0	2	0	0	2	-	1	0	1	0	1	0	0	1	1	2	1	0	0	0	0	0	0
-	1	-	-	1	3	0	0	1	-	3	0	1	1	1	0	0	0	0	-	1	0	0	0	0	1	0
-	1	-	-	1	3	0	0	1/2	-	3	0	1	1	1	0	0	0	0	-	1	0	0	0	2	1	0
-	-	-	-	?	2/4	0	0	1/2	-	4	?	0/1	?	1	0	0	0	0	-	1	0	1	0	0	0	0
0	-	-	-	0	2	1	0	2	1	1	0	0	-	1	0	0	1	0	-	0	0	0	0	0	0	0
0	-	-	-	?	2/4	1	?	-	?	1/3/4	?	0	-	1	0	0	1	0	-	1	0	0	0	0	0	0
-	-	-	-	?	2/4	?	?	?	?	1/3/4	?	0/1	?	1	0	0	0	0	-	1	0	0	0	2	0	0

Appendix III

A priori *weights applied to the initial analyses for A/Pe and A/Pw*

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
A/Pe	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
A/Pw	1	1	1	1	1	1	1	1	1	1	0.5	0.5	1	0.5	0.25	0.25	0.125	0.125	0.125	0.125	0.125

Character	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
A/Pe	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
A/Pw	0.5	0.25	0.25	1	0.5	0.5	0.5	1	1	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5

Character	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
A/Pe	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
A/Pw	0.5	1	0.5	0.5	0.5	0.5	0.5	0.5	0.25	0.25	0.25	0.25	0.5	1	1	1	1	1	1	1	1

Character	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
A/Pe	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
A/Pw	1	1	1	1	1	1	1	1	1	1	0.5	0.25	0.25	0.25	0.5	0.5	0.5	0.5	0.25	0.25	1

Character	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
A/Pe	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
A/Pw	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Character	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124
A/Pe	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
A/Pw	0.5	0.5	0.5	0.5	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5

Appendix IV

Justification and discussion of scores in both A/P and multistate matrices

Character numbers refer to that of A/P coding. In multistate coding, autapomorphic states have been included, and the relevant states can be found in Appendix 1. For A/P coding, autapomorphies have not been included, but the relevant character can be found as a state in multistate coding. Some new observations have been included, mostly on chaetal distribution and structure and on other external features, such as branchiae, nephridial and genital openings. For A/P character 68, Dorsolateral folds, the justifications are based on Purschke & Tzetlin (1996: table 2 and text). Where Purschke & Tzetlin (1996: table 2) indicated a taxon as being both absent or present the group is scored in Appendix II as present. The Clitellata are scored with dorso-lateral folds based on arguments in Purschke & Tzetlin (1996: 47). Twelve ingroup taxa (e.g. Myzostomidae, Aeolosomatidae) could not be scored and are left as unknown. Sipuncula, Echiura, Onychophora, and Euarthropoda were scored absent for this character.

Sipuncula. General references: Hyman (1959); Rice (1975, 1993); Cutler (1994).
  Head structure. 1–4. Prostomium. The region in front of the prototroch (the prostomium) develops into the tentacles in *Golfingia* spp. (see Hyman 1959: fig. 238B). It is assumed here that this is the general case for the group and cannot be regarded as homologous with any other condition referred to here; thus, they are given their own state in multistate coding.
  5–9. Peristomium. The peristomium, if it can be considered present, can also not be regarded as homologous with any other conditions described here. The buccal region would appear to migrate (Hyman 1959: 657) to a terminal position, and any peristomial material is thus immediately below, or completely surrounded by, the prostomial tentacles (see Rice 1993: figs 16-21, 80, 81).
  13–24. Palps. Though grooved, the sipunculid tentacles do not appear to be homologous with palps (see description by Rice 1993: 267).
  25–28. Nuchal organs. Nuchal organs are regarded as absent, mainly due to the fact that they are single structures rather than paired (see Rice 1993: 307, figs 165–170; Rouse & Fauchald 1995: 276).
  Trunk structures. 29–30. Segmentation and muscle bands. Muscle banding is considered absent. Some groups have multiple banding, but this is considered a derived state within the group (Cutler 1994).
  Digestive system. 66–72. Stomodaeum. The structure of the sipunculid 'pharynx' is not considered homologous with any other taxa under consideration here, and they are given their own state in multistate coding (see Rice 1993: 266–269).
  84–88. Gular membrane and gut. The tightly coiled gut and non-terminal anus of sipunculids are considered a separate state in multistate coding (Stephen & Edmonds 1972: 347; Rice 1993: figs 10–15).
  Excretory/reproductive system. 89–95. Nephridial structures. Metane-phridia are present, but any coelomoduct involvement is unknown, though they do act as gonoducts (Hyman 1959; Rice 1993).
  96–99. Organisation/distribution of segmental organs. The single pair (exceptionally only one nephridium) found in Sipuncula (Rice 1993: 291–292) does not appear to be homologous with any other condition under consideration here.
  100. Sperm morphology. No mitochondrial interpolation (Rice 1993: figs 199–202).
  Circulation. 101–104. Circulation and heart body. Circulatory system is absent (Rice 1993: 275; Cutler 1994).
  Chaetal structures. 105–124. Chaetae. Absent.

Echiura. General references: Stephen & Edmonds (1972); Pilger (1993).
  Head structure. 1–4. Prostomium. Own state in multistate coding. The proboscis of the Echiura appears to be the prostomium (Stephen & Edmonds 1972: figs 42a, c; Pilger 1993: 185).
  5–9. Peristomium. Is limited. The position of prototroch remnants and septum separating the body cavity from the head justifies this score (Newby 1940).
  25–28. Nuchal organs. None has been reported. Bullock & Horridge (1965: 656–658) did not mention any anterior sensory organs other than sensory papillae along the edge of the proboscis.
  Trunk structures. 29–30. Segmentation and muscle bands. Both are absent (see Pilger 1993).
  44–55. Parapodial structures. Absent.
  60–65. Sensory structures, papillae and pygidial cirri. Papillae are present (Stephen & Edmonds 1972) but not of the construction intended by this character.
  Digestive system. 66–72. Stomodaeum. The structure of the echiuran pharynx is not considered homologous with any other taxa under consideration here and they are given their own state in multistate coding (see Pilger 1993: 211).
  84–88. Gular membrane and gut. The coiled gut of the Echiura is considered a separate state in multistate coding and to not be homologous with the sipunculid condition (see Stephen & Edmonds 1972: 347; Pilger 1993: fig. 1B).
  Excretory/reproductive system. 89–95. Nephridial structures. Metane-phridia are present, 'probably' as mixonephridia (Goodrich 1945: 232). The Echiura are coded as '?' for the relevant characters since no developmental evidence is available.
  96–99. Organisation/distribution of segmental organs. Depending on the species, the Echiura can have from one to 400 metanephridia (Stephen & Edmonds 1972: 353; Pilger 1993: 214). The echiuran state is not considered homologous with other taxa (though similarities with Sipuncula should be investigated), and they are given their own state for this character (see Goodrich 1945: 230–233). The origin of the excretory 'anal sacs' deserves further investigation.
  100. Sperm morphology. Mitochondria not interpolated (Pilger 1993).
  Circulation. 101–104. Circulation and heart body. Closed circulation except in one group (Pilger 1993: 206). No heart body.

Chaetal structures

105–124. Chaetae. Chaetae are chitinous, falcate hooks (Storch 1984; Pilger 1993).

Euarthropoda. General references: Brusca & Brusca (1990); Wheeler *et al.* (1993).

Head structure. 1–4. Prostomium. Forms acron (Brusca & Brusca 1990).

5–9. Peristomium. Forms acron (Brusca & Brusca 1990).

10–12. Antennae. Are segmental and hence not homologous with prostomial antennae.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present (Brusca & Brusca 1990: 465, fig. 2; Wheeler *et al.* 1993.

31–43. First segment structure and appendages. The first segment in arthropods varies within the group in terms of appendages and degrees of fusion but that are scored with their own state that is also shared with Onychophora (see Brusca & Brusca 1990: 669). This is justifiable since the various arthropod states would all appear to be more similar with each other than to any of the other conditions outlined here.

44–55. Parapodial structures. Absent.

56–59. Gills or branchiae. Not homologous with any of the conditions discussed here.

Digestive system. 66–72. Stomodaeum. The euarthropod stomodaeum cannot be considered to be homologous with any of the other states considered here, so they have their own state, shared with the Onychophora.

84–88. Gular membrane and gut. Gular membrane is absent, gut is straight (Brusca & Brusca 1990: 477).

Excretory/reproductive system. 89–95. Nephridial structures. Euarthropods have metanephridial derivatives, but there is no evidence to consider them mixonephridia or metanephromixia (see Nielsen 1995: 166; Rouse & Fauchald 1995: 276).

96–99. Organisation/distribution of segmental organs. The dorsal gonads of arthropods are considered to be homologous with those of the Onychophora (Wheeler *et al.* 1993).

100. Sperm morphology. No mitochondrial interpolation (Jamieson 1986).

Circulation. 101–104. Circulation and heart body. Circulation is an open system with an ostiate heart (see Rouse & Fauchald 1995: 277).

Chaetal structures. 105–124. Chaetae. Absent.

Onychophora. General references: Anderson (1973); Brusca & Brusca (1990); Storch & Ruhberg (1993).

Head structure. 1–4. Prostomium. Absent; the acron present in arthropods which is the fused prostomium and peristomium is completely absent in the onychophorans (Anderson 1973).

5–9. Peristomium. Absent. See above.

10–12. Antennae. The head of the Onychophora appears to be a segmental structure (Anderson 1973: 121), and hence their antennae cannot be considered homologous with those found in many polychaetes.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present (Storch & Ruhberg 1993: fig. 2).

31–43. First segment structure and appendages. The first segment bears antennae (Brusca & Brusca 1990: 668).

44–55. Parapodial structures. Onychophoran lobopods are not considered homologous with parapodia (Manton 1967).

Digestive system. 66–72. Stomodaeum. The onychophoran stomodaeum seems to more similar to a euarthropod condition than to any of the other characters considered.

84–88. Gular membrane and gut. A gular membrane is absent and the gut is straight (Brusca & Brusca 1990: 671).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present and fused to coelomic remnants (Brusca & Brusca 1990: 671–672, fig. 5A) but cannot be considered mixonephridia.

96–99. Organisation/distribution of segmental organs. While the accessory genital glands of Onychophora, like the salivary glands, appear to be modified nephridia (Storch & Ruhberg 1993), there is no evidence that the gonoducts themselves have a nephridial component, although Nielsen (1995: 154) suggests that this is the case. The dorsal gonads of the Onychophora are a synapomorphy with euarthropods (Wheeler *et al.* 1993), and these taxa have their own character.

100. Sperm morphology. Mitochondria are interpolated between the nucleus and the axoneme (Jamieson 1986).

Circulation. 101–104. Circulation and heart body. Circulation is an open system with an ostiate heart (see Rouse & Fauchald 1995: 277).

Chaetal structures. 105–124. Chaetae. Absent.

Frenulata. General references: Ivanov (1963); Southward (1980, 1988, 1993), Rouse & Fauchald (1995).

Head structure. 1–4. Prostomium. Called cephalic lobe in Southward (1980, 1993). Is distinct from the peristomium (see Rouse & Fauchald 1995: 287).

5–9. Peristomium. Part of the forepart in Southward (1980, 1993). Is elongate compared with other taxa (see Rouse & Fauchald 1995: 287).

13–24. Palps. Called tentacles in Southward (1993). Arising behind the prototroch, the position and morphology of these structures are strikingly similar to the peristomial grooved palps of many polychaete groups and (see Bakke 1980; Southward 1988; Callsen-Cencic & Flügel 1995). It is assumed here that the plesiomorphic condition for the group is to have a pair of palps as in the genera *Nereilum, Siboglinoides, Diplobrachia* (Ivanov 1963: 164, 327, 373) and *Sclerolinum* (Ivanov 1963: 420; Webb 1964), though this requires further investigation. *Polybrachia canadensis*, a multiple palp bearing species shown by Southward (1971), initially has a single palp, and this condition is found in many adults of other species (e.g. *Siboglinum* spp.). Further study is clearly needed.

25–28. Nuchal organs. No evidence for nuchal organs has been found, but the matter is unresolved (Rouse & Fauchald 1995).

Trunk structures. 29–30. Segmentation and muscle bands. Present (see Rouse & Fauchald 1995).

31–43. First segment structure and appendages. What is here interpreted as the first segment is termed the trunk in Southward (1993). It begins behind the diaphragm and is extremely elongate. The first segment bears rows of uncini in what is interpreted here as tori (see Ivanov 1963: fig. 31; Southward 1993: fig. 4). Tori are not present in the segments of the opisthosoma, so the first segment does differ from the following ones. The Frenulata have their own state for this character under multistate coding.

44–55. Parapodial structures. As stated for the 'First segment appendages', Ivanov (1963: fig. 31) is interpreted here as providing evidence that the Frenulata have tori with uncini (see also Bartolomaeus 1995). However, the segments of the opisthosoma differ from this interpretation and cannot be termed parapodia (Southward 1993: figs 13, 14).

Digestive system. 66–72. Stomodaeum. A transient stomodaeum is present in larvae (Callsen-Cencic & Flügel 1995). It is absent in adults.

84–88. Gular membrane and gut. Southward (1993: 341) referred to the first septum as being structurally different from the opisthosomal septa. This is considered to be homologous with gular membranes, though further investigation is warranted. The gut lumen in the Frenulata is occluded. Southward (1993: 351) reported the presence of a central lumen in the trophosome and referred to it as a remnant gut lumen.

Excretory/reproductive system. 89–95. Nephridial structures. Southward (1980) reported protonephridia in two species of Frenulata. Callsen-Cencic & Flügel (1995) report similar structures in the larvae of *Siboglinum poseidoni* and suggest that they are present in the adults.

96–99. Organisation/distribution of segmental organs. A single pair of excretory organs is present anteriorly in all Frenulata (Ivanov 1963). The gonads empty through separate openings posteriorly and this is interpreted here as similar to that system found in many polychaetes (see also Bartolomaeus 1995).

100. Sperm morphology. Mitochondria not interpolated (Southward 1993).

Circulation. 101–104. Circulation and heart body. Circulation closed, a heart is present (Ivanov 1963; Southward 1993: 345–346). A structure termed the corpus cardiacum by Ivanov (1963: 76–77) may be a heart body but requires further investigation.

Chaetal structures. 105–124. Chaetae are present and chitinous (see Rouse & Fauchald 1995). Bartolomaeus (1995) provides firm evidence that the girdle chaetae of the first segment are uncini.

Vestimentifera. General reference: Gardiner & Jones (1993).

Head structure. 1–4. Prostomium. A prostomium in vestimentiferans is present in larvae (Gardiner & Jones 1993: fig. 35; Southward 1993: fig. 29). In adults, however, it is difficult to identify, and further study is required. Interpreted here as being fused to the peristomium and reduced as in groups like the Sabellidae and Serpulidae.

5–9. Peristomium. Called the vestimentum in Gardiner & Jones (1993). Is elongate compared with other taxa.

13–24. Palps. Called tentacles or branchial filaments by other authors. As in the Frenulata, the development and morphology of these structures is strikingly similar to the peristomial grooved palps of many polychaete groups (see Southward 1988: figs 4–5; Gardiner & Jones 1993: figs 35, 36). All vestimentiferans have numerous palps, though they initially have only a single pair.

25–28. Nuchal organs. No evidence for nuchal organs has been found, but the matter is unresolved (Rouse & Fauchald 1995).

Trunk structures. 29–30. Segmentation and muscle bands. Present (see Rouse & Fauchald 1995).

31–43. First segment structure and appendages. What is here interpreted as the first segment is termed the trunk in Gardiner & Jones (1993). It begins behind the diaphragm and is extremely elongate. No appendages are present. Chaetae are present in larval vestimentiferans but are later lost (Gardiner & Jones 1993: figs 35, 36).

44–55. Parapodial structures. While no appendages are present on the

first segment, the structures bearing the uncini in the opisthosoma are interpreted here as tori (see Bartolomaeus 1995).

Digestive system. 66–72. Stomodaeum. A transient stomodaeum is present in larvae. It is absent in adults (Jones & Gardiner 1988; Southward 1988).

84–88. Gular membrane and gut. No evidence for gular membrane. The gut lumen in the Vestimentifera is occluded, as in the Frenulata (Gardiner & Jones 1993).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present (see Rouse & Fauchald 1995). Nephromixia cannot be resolved on present evidence.

96–99. Organisation/distribution of segmental organs. A single pair of excretory organs is present anteriorly in vestimentiferans. The gonads empty through separate openings posteriorly, and this is interpreted here as similar to the system found in many polychaetes (see also Bartolomaeus 1995).

100. Sperm morphology. Mitochondria not interpolated (Gardiner & Jones 1993).

Circulation. 101–104. Circulation and heart body. Closed circulation, a 'heart region' is present (Gardiner & Jones 1993: 399), but a heart body appears to be absent.

Chaetal structures. 105–124. Chaetae. Are present and chitinous (see Rouse & Fauchald 1995). Capillary chaetae are present in larval stages (Gardiner & Jones 1993: figs 35, 36). Bartolomaeus (1995) provides firm evidence that the girdle chaetae of the first segment are uncini.

Clitellata. General references: Stephenson (1930); Cook (1971).

Head structure. 1–4. Prostomium. Is distinct from the peristomium (Stephenson 1930: figs 1, 30–32).

5–9. Peristomium. Forms a complete ring (Anderson 1971: 101).

25–28. Nuchal organs. Are considered absent (see Rouse & Fauchald 1995).

Trunk structures. 29–30. Segmentation and muscle bands. Present (see Rouse & Fauchald 1995).

31–43. First segment structure and appendages. Is similar to those of the rest of the body.

44–55. Parapodial structures. Clitellates lack parapodia. Stephenson (1930: 716 and following) suggested that chaetae are moved by musculature similar to those in the polychaetes, but are not elevated on structures corresponding to the parapodia.

56–59. Gills or branchiae. Are present in some taxa such as naiads, tubificids, phreodrilids and glossoscolecids but do not correspond to any of the forms discussed here.

60–65. Sensory structures, papillae and pygidial cirri. The lateral line of the clitellates is similar positionally to lateral organs; however, functionally and histologically, they are different (Jeener 1928: 117).

Digestive system. 66–72. Stomodaeum. The dorsally muscularised pharynx found in the Clitellata (Cook 1971: 22, Purschke & Tzetlin 1996) is an autapomorphic feature in multistate coding.

84–88. Gular membrane and gut. Stephenson (1930: 52) states anterior septa may be muscularised, but anterior septa resemble each other and change slowly in shape with position in the body. The gut is straight except in hirudineans.

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present and are not associated with coelomoducts (Goodrich 1945: 234, 280).

96–99. Organisation/distribution of segmental organs. The nephridial/genital system in the Clitellata is not considered homologous with any other system on present evidence and they are given their own state in multistate coding (Goodrich 1945: 280).

100. Sperm morphology. Mitochondria interpolated (see Rouse & Fauchald 1995).

Circulation. 101–104. Circulation and heart body. Closed circulation, heart body absent (Cook 1971).

Chaetal structures. 105–124. Chaetae. Capillary chaetae and spines are present in many microdriles (Stephenson 1930: 8–12; Cook 1971: 12–15). While hook-like structures can be interpreted in clitellates (Stephenson 1930: 10), they are not regarded as homologous with the hooks considered here.

Aberrantidae. General reference: (Wolf 1987).

Head structure. 1–4. Prostomium. Distinct (Wolf 1987: fig. 1a).

5–9. Peristomium. Interpreted here as forming two rings. Wolf (1987: 50) suggests that the first two achaetigerous segments may be the peristomium (see also Hobson 1971: fig. 1c; Wolf 1987: fig. 1a, 1b; Mackie *et al.*, in prep.).

10–12. Antennae. The antennae of aberrantids are considered homologous to other prostomial antennae (Mackie *et al.*, in prep.).

13–24. Palps. The ventral grooved palps of aberrantids are not homologous with grooved palps of other taxa. They are considered to be similar to palps of taxa such as dorvilleids (Mackie *et al.*, in prep.).

25–28. Nuchal organs. Probable nuchal organs illustrated as comma-shaped structures, located slightly dorsal and posterior to palps in Wolf (1987: fig. 1b) and as paired dorsolateral comma-shaped structures in Hobson (1971).

Trunk structures. 29–30. Segmentation and muscle bands. Presence of muscle bands based on Mackie *et al.* (in prep.).

31–43. First segment structure and appendages. The first segment is similar to the remainder of the body and has similar appendages if the achaetous segments of Wolf (1987) are interpreted as peristomial.

44–55. Parapodial structures. Neuropodia project (Hartman 1965: pl. 32, fig. h). Cirri are absent. The large flattened parapodial lobes are considered postchaetal by Wolf (1987).

56–59. Gills or branchiae. Present dorsally. Distinctly separated from notopodia and strap-like according to Wolf (1987).

60–65. Sensory structures, papillae and pygidial cirri. A single pair of pygidial cirri are present (Hobson 1971: fig. 1e).

Digestive system. Under investigation (Mackie *et al.*, in prep.).

Excretory/reproductive system. Under investigation (Mackie *et al.*, in prep.).

Circulation. 101–104. Circulation and heart body. Circulation unknown. Heart body not noted previously and assumed to be absent.

Chaetal structures. 105–124. Chaetae. Capillary chaetae are the only chaetal type found relevant to this character set.

Acoetidae. General references: Pettibone (1989); Orrhage (1991).

Head structure. 1–4. Prostomium. Distinct (Pettibone 1989: fig. 1a).

5–9. Peristomium. Forms lips only (Pettibone 1989: fig. 28b).

10–12. Antennae. Three prostomial antennae are present (Pettibone 1989: fig. 1a).

13–24. Palps. A pair of ventral palps is present (Orrhage 1991; Pettibone 1989: figs 1a, 28a).

25–28. Nuchal organs. Pruvot & Racovitza (1895: 446) mention that the posterior part of the brain innervated, 'as always' the nuchal organs.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present (Clark 1962: fig. 4; Storch 1968: 268, fig. 4).

31–43. First segment structure and appendages. Surrounds the head with parapodia similar to the rest of the body (Pettibone 1989: fig. 13a). Two pairs of tentacular cirri (Pettibone 1989: fig. 1a).

44–55. Parapodial structures. Neuropodia project (Pettibone 1989: figs 2–3). Dorsal cirri present, cirriform and elytra (Pettibone 1989: figs 2e, 8d–h). Ventral cirri cirriform (Pettibone 1989: fig. 2e).

56–59. Gills or branchiae. Scored absent (on parapodia in only a few taxa).

60–65. Sensory structures, papillae and pygidial cirri. A single pair of pygidial cirri (Pettibone 1989: 7).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Two pairs of jaws (Fauvel 1923: fig. 37a; Dales 1962; Pettibone 1989: 9).

84–88. Gular membrane and gut. No gular membrane reported. Side branches present (Storch 1968: fig. 4).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia assumed based on Goodrich's (1945) review as a generalisation for all scaleworms. Other features unknown.

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Aciculae and capillary chaetae and spines are present (Pettibone 1989: 7–10). Fine silk notochaetae are present. A description of spinning glands is in Pflugfelder (1934).

Acrocirridae. General reference: Banse (1969); (Okuda 1934).

Head structure. 1–4. Prostomium. Distinct (Banse 1969: fig. 1a–b).

5–9. Peristomium. As lips only (Okuda 1934: fig. 2b).

13–24. Palps. Banse (1969: 2596) discussed the position of the anterior pair of palps and was unable to decide whether they were prostomial or peristomial. They are here considered peristomial grooved palps, based in part on personal observations.

25–28. Nuchal organs. Present (Okuda 1934: 198).

Trunk structures. 29–30. Segmentation and muscle bands. Segmentation present. Muscle bands unknown.

31–43. First segment structure and appendages. Banse (1969: 2596, fig. 1b) referred to what is here called the first segment as the second segment. It is similar to other segments but lacks parapodia and chaetae and carries the first pair of gills.

44–55. Parapodial structures. Parapodia of some taxa have larger notopodia, but in most the two rami are similar. No cirri are present. Some of the many papillae may be in the position of a dorsal cirrus, but do not appear to differ structurally from the other papillae (Fauchald pers. obs.).

56–59. Gills or branchiae. Are dorsal, usually limited to four pairs anteriorly (Banse 1969: 2596).

60–65. Sensory structures, papillae and pygidial cirri. Epidermal papillae are present (Okuda 1934; Mesnil 1899).

Digestive system. 78–83. Ventral pharynges and associated structures.

A ventral buccal bulb is present. It was termed a proboscis, so it is assumed here to be eversible (Banse 1969: 2596).

84–88. Gular membrane and gut. Gular membrane unknown. Gut a straight tube (Okuda 1934: 201–202).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia, and the description in Okuda (1934: 201, 206) matches those of mixonephridia in cirratulids (note that the acrocirrids at the time were assumed to be cirratulids).

96–99. Organisation/distribution of segmental organs. Anterior excretory pair noted by several authors (Marion & Bobretzky 1875; Mesnil 1899; Banse 1969: 2597). Okuda's (1934) observation of numerous anterior nephridia requires further investigation. Gametes are posteriorly located (Okuda 1934: 201, 206), and it is assumed that posterior gonoducts are present.

100. Sperm morphology. No mitochondrial interpolation (Sawada 1984).

Circulation. 101–104. Circulation and heart body. Circulation is closed since a heart body is present (Mesnil 1899; Okuda 1934: 202).

Chaetal structures. 105–124. Chaetae. Hooked compound chaetae with a fold, and capillary chaetae are present (Banse 1969).

Aeolosomatidae. General references: Bunke (1967, 1988).

Head structure. 1–4. Prostomium. Fused but distinct (Bunke 1967: figs 2–3).

5–9. Peristomium. Lips only (Bunke 1967: 196). Bunke's 'Pharynxabschnitt' is here considered peristomial.

25–28. Nuchal organs. Are clearly present (Bunke 1967: 196, fig. 1b).

Trunk structures. 29–30. Segmentation and muscle bands. Segmentation present. Muscle banding appears absent (see Marcus 1944: fig. 23).

31–43. First segment structure and appendages. All segments are similar with similar appendages (Bunke 1967: fig. 1a).

44–55. Parapodial structures. They are considered absent here, and there are hence no associated appendages.

Digestive system. 78–83. Ventral pharynges and associated structures. An eversible ventral buccal bulb is present (Bunke 1967: 196–197, fig. 33a, b).

84–88. Gular membrane and gut. Gular membrane absent. Bunke (1988: 345) indicated that septa were reduced except for the first (presumably between the peristomium and the first segment); however, there is no indication that this complete septum is muscularised in the fashion of a gular membrane. Gut a straight tube (Bunke 1988: 346).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia described by Bunke (1994). Based on Bunke's (1994: 257) finding that there is a mesodermal component to the aoelosomatid metanephridia, they are considered here to be mixonephridia. This requires further investigation.

96–99. Organisation/distribution of segmental organs. In most segments. Bunke (1988: 345; 1994) stated that the metanephridia are not present in all segments; however, male gonads are present anterior and posterior to the female ones and sperm is voided through the metanephridia, thus segmental organs must be present at least in a majority of the segments.

100. Sperm morphology. Mitochondria not interpolated (Bunke 1986).

Circulation. 101–104. Circulation and heart body. Circulation is closed (Baskin 1928; Marcus 1944; Hanson 1949). Heart body is absent (Bunke 1967: fig. 32).

Chaetal structures. 105–124. Chaetae. Capillary chaetae are the only ones relevant to the characters here. The sigmoid chaetae present in some taxa are shorter, distally truncate, with teeth or rugosities and might qualify as spines or hooks.

Alciopidae. General references: Dales (1955); Rice (1987); Wu & Lu (1994).

Head structure. 1–4. Prostomium. Distinct groove (Rice 1987: figs 1–3).

5–9. Peristomium. Limited to lips (Rice 1987: fig. 1a).

10–12. Antennae. A lateral pair and median antennae are present.

13–24. Palps. The ventral pair of what is traditionally called two pairs of frontal antennae are here considered palps. Further investigation is required (see Phyllodocidae).

25–28. Nuchal organs. Present, Claparède (1870: pl. 10, fig. 1) illustrates ciliated patches around bases of the eyes.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segment is indistinct with tentacular cirri only (Rice 1987: 116, figs 1–3).

44–55. Parapodial structures. Rice (1987: 118) referred to the parapodia as uniramous. The foliose dorsal cirri are here considered representing the notopodia as in the phyllodocids. Ventral cirri are also present.

60–65. Sensory structures, papillae and pygidial cirri. One pair of pygidial cirri (Apstein 1891: figs 5, 15).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Jaws are absent (Dales 1962; Rice 1987: 115, figs 2a–f).

84–88. Gular membrane and gut. Gular membrane absent, gut straight (Claparède 1870: pl. 10, fig. 1).

Excretory/reproductive system. 89–95. Nephridial structures. Protonephridia as protonephromixia (Goodrich 1912b, 1945: 155–157).

96–99. Organisation/distribution of segmental organs. Coded as along the body, though some anterior segments are not reproductive (Claparède 1870: 470; Goodrich 1900,1912b).

100. Sperm morphology. Mitochondria not interpolated (Rice 1992).

Circulation. 101–104. Circulation and heart body. Circulatory system limited (Smith & Ruppert 1988: 234).

Chaetal structures. 105–124. Chaetae.

Aciculae, tapering compounds with a single ligament and capillary chaetae are present. Compounds are absent in many species but presence is assumed to be the plesiomorphic condition based on Wu & Lu (1994).

Alvinellidae. General reference: Desbruyères & Laubier (1991).

Head structure. 1–4. Prostomium. Distinct groove (Desbruyères & Laubier 1991: fig. 3a–b).

5–9. Peristomium. May be internalised, forming the roof of the mouth and perhaps the lower lip. (Desbruyères & Laubier 1991, fig. 3c).

13–24. Palps. It is assumed here that what Desbruyères & Laubier (1991: 32) call ciliated grooved (buccal) tentacles correspond to the structures present in pectinariids and possibly ampharetids and that these structures are multiple peristomial grooved palps.

25–28. Nuchal organs. Desbruyères & Laubier (1991: fig. 3a) show a ciliated transverse patch in the correct position.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

34–47. First segments structure and appendages. First two to three segments fused, separated from the head by a distinct groove. The first segment has no appendages apart from gills (Desbruyères & Laubier 1989: fig. 1b).

44–55. Parapodial structures. Tori are present (Desbruyères & Laubier 1980: figs 4–6; 1991: 32). Desbruyères & Laubier (1991: 33) refer to dorsal notopodial (digitiform) lobes present in *Paralvinella*; these may be dorsal cirri, but they are scored here as absent.

56–59. Gills or branchiae. Present, dorsal and branched. Always four anterior pairs (Desbruyères & Laubier 1991: 32).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are unknown; other features are absent.

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral non-eversible buccal bulb is present (Desbruyères & Laubier 1991: 32). The dorsal modifications of the stomodaeal regions appear to be apomorphic for the family.

84–88. Gular membrane and gut. Gular membrane present between two anterior segments. The digestive tract appears to be looped as in the ampharetids, but better documentation is needed (Fauchald pers. obs., specimen USNM 120715).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present (Zal *et al.* 1994: 43), and the structures are described in such a fashion as to imply that one anterior pair of ducts are strictly nephridial and the next three pairs are gonadal in function. This is similar to the kinds of structure present in ampharetids and terebellids, and hence they are classifiable as mixonephridia.

96–99. Organisation/distribution of segmental organs. Organisation is similar to ampharetids. See preceding comment.

100. Sperm morphology. Mitochondrial interpolation present (McHugh 1995b).

Circulation. 101–104. Circulation and heart body. A circulatory system is present (Fauchald pers. obs., specimen USNM 120715); it is here assumed to be closed. No heart body noted, but could be present.

Chaetal structures. 105–124. Chaetae. Capillary chaetae, uncini, and spines in an anterior chaetiger are present. Desbruyères & Laubier (1991) refer to the modified notopodial chaetae present in an anterior segment as hooks; they are more appropriately called spines.

Ampharetidae. General references: Hessle (1917); Day (1964); Holthe (1986a, b).

Head structure. 1–4. Prostomium. Distinct (Hessle 1917: pl. 1, figs 5–8).

5–9. Peristomium. Limited to lips. Day (1964) argued that the anterior achaetous region is segmental.

13–24. Palps. Ampharetids have buccal tentacles located on a dorsally attached curtain within the buccal cavity; occasionally, these tentacles are supplemented by a single or a pair of large, grooved palps (Hartman 1969: 548–549, fig. 2, 570–571, fig. 1). The buccal tentacles are here considered peristomial palps.

25–28. Nuchal organs. Present (Hessle 1917: 85; Rullier 1951: 309).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Meyer 1887; Fauvel 1897; Storch 1968: fig. 27).

31–43. First segment structure and appendages. Day (1964: 99) reviewed the construction of the anterior end of the ampharetids, concluding that the paleal segment (when paleae are present) is the third

segment in agreement with Fauvel (1927: 225). This hypothesis is accepted here, leaving the first segment achaetigerous and completely fused to the head and has no appendages.

44–55. Parapodial structures. Tori are present (Holthe 1986a: fig. 8b). The cirri attached at the upper edge of the neuropodia in the abdomen of certain ampharetids (Holthe 1986a: fig. 8b) appear to be *de-novo* structures not related to dorsal cirri associated with the notopodia.

56–59. Gills or branchiae. The family is scored as having dorsal branchiae homologous to other terebellimorphs. Up to four pairs of tapering branchiae are present in most taxa; in some of the taxa (e.g. *Isolda, Pterampharete*) one or more pairs of branchiae may be pinnate; in some species (e.g. *Amphicteis scaphobranchiata*, one pair may have a subdistal flattened region (Hartman 1969: 548–549: fig. 1).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are present (Rullier 1951: 303). Multiple pygidial cirri can be present (Uschakov 1955: 360; Holthe 1986a).

Digestive system. 78–83. Ventral pharynges and associated structures. Holthe (1986a: 44) discusses the buccal tentacles among the terebellimorphs; it is not clear from his discussion what the structure of the lower lip is. Fauvel (1897) demonstrated the presence of a non-eversible buccal organ in the family. Dales (1963: 65) refers to the buccal organ as a lip and food sorter. Purschke & Tzetlin (1996: fig. 10D) also show a ventral buccal organ but do not discuss eversibility.

84–88. Gular membrane and gut. Gular membrane present (Meyer 1887; Hessle 1917). The gut is straight in *Melinna*, but looped in *Amphicteis*; scored as being looped for the family (Wirén 1885: 30–31).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia (Goodrich 1945: 192, fig. 46).

96–99. Organisation/distribution of segmental organs. As in other terebellimorphs, there are a few anterior pairs of segmental organs with the first of these being excretory only (Goodrich 1945: 192).

100. Sperm morphology. No interpolation of mitochondria (McHugh & Tunnicliffe 1994).

Circulation. 101–104. Circulation and heart body. Circulation is closed (Wirén 1885: 15–17). Heart body is present (Picton 1899; Kennedy & Dales 1958).

Chaetal structures. 105–124. Chaetae. Are present in the form of capillaries, anterior spines and uncini.

Amphinomidae. General reference: Gustafson (1930).

Head structure. 1–4. Prostomium. Is distinct (Gustafson 1930: 372).

5–9. Peristomium. Limited to lips (Gustafson 1930: pl. 27, fig. 7).

10–12. Antennae. A pair of antennae are located on the anterior lobe of the prostomium; the median antenna on the posterior lobe (Gustafson 1930: fig. 38).

13–24. Palps. Present ventro-laterally (Gustafson 1930: 372, 378; Orrhage 1990).

25–28. Nuchal organs. Storch & Welsch (1969: 1335) demonstrated that caruncles are nuchal organs.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Gustafson 1930; pl. 3, fig. 5; Storch 1968: fig. 21).

31–43. First segment structure and appendages. Dorso-lateral around head with parapodia similar to those in the remainder of the body (Gustafson 1930: pl. 1).

44–55. Parapodial structures. Parapodia with similar rami (Day 1967: fig. 3.2). Cirriform dorsal and ventral cirri are present (Kudenov 1993: figs 1a, 2a).

56–59. Gills or branchiae. Parapodial gills are present at the base of the notopodia (Gustafson 1930: 313).

60–65. Sensory structures, papillae and pygidial cirri. Pygidial cirri are absent (Marsden 1963: 177).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral hypertrophied pharynx with a thickened, ridged cuticle is present (Gustafson 1930: 401–404; Dales 1962; Marsden 1963: 168; Purschke & Tzetlin 1996: fig. 5).

84–88. Gular membrane and gut. No gular membrane. Gut a straight tube (Gustafson 1930: 400–410).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia (Goodrich 1900; 1945: 187; Gustafson 1930: 412, pl. 36, fig. 5).

96–99. Organisation/distribution of segmental organs. Not specifically mentioned; however, since no restriction on distribution has been mentioned, it is assumed to be distributed along the body.

100. Sperm morphology. Mitochondria not interpolated (Rouse & Jamieson 1987).

Circulation. 101–104. Circulation and heart body. Circulatory system. Closed circulation, no heart body (Gustafson 1930: 411).

Chaetal structures. 105–124. Chaetae. Have a calcareous component. Aciculae, capillary chaetae and spines are present.

Aphroditidae. General references: Darboux (1899); Fordham (1926).

Head structure. 1–4. Prostomium. Distinct groove (Fordham 1926: pl. 2, fig. 3).

5–9. Peristomium. Limited to lips, Fordham (1926: 129, Textfig. 1) interpreted the first segment as part of the peristomium.

10–12. Antennae. A median antenna only is present (Fordham 1926: 127, pl. 2, fig. 3).

13–24. Palps. Ventral palps are present (Fordham 1926: 27, pl. 2, fig. 3).

25–28. Nuchal organs. Present (Hanström 1928: 262–264, fig. 268; Rullier 1951: 309).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Darboux 1899: 154; Storch 1968: fig. 2a).

44–55. First segment structure and appendages. Surrounds the head with parapodia similar to the rest of the body (Fordham 1926: pl. 2, fig. 3; Fauchald 1977: fig. 14). Tentacular cirri present (Fordham 1926: pl. 2, fig. 3).

44–55. Parapodial structures. Neuropodia project (Fordham 1926: 130–133, pl. 2, fig. 6). Dorsal cirri are present, both cirriform and as elytra (Fordham 1926: 135, 139). Ventral cirri present (Fordham 1926: 131, 135, pl. 2, fig. 6).

56–59. Gills or branchiae. Fordham (1926: 154) assigns respiratory function to the dorsal body-wall and the elytra, but does not describe the presence of any distinctly respiratory structures.

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri (Fauvel 1923: 34), but see Fordham (1926: pl. 4, figs 32, 35).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Two pairs of jaws (Fordham 1926: 160–161, 167, Textfig. 8; pl. 1, fig. 2; Dales 1962).

84–88. Gular membrane and gut. Fordham (1926) does not mention any differentiation of anterior septa. Gut side branches present (Darboux 1899; Fordham 1926: 163).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia (Darboux 1899: 245–252; Goodrich 1945: 187). Ciliophagocytal organs are absent (Goodrich 1945).

96–99. Organisation/distribution of segmental organs. In most segments (Darboux 1899: 245–252; Fordham 1926: 186; Goodrich 1945: 187).

Circulation. 101–104. Circulation and heart body. Closed with no heart body (Fordham 1926: 151–154; Hanson 1949).

Chaetal structures. 105–124. Chaetae. Aciculae and capillary chaetae and spines are present. Spinning glands producing fine silky notochaetae are also present.

Apistobranchidae. General references: Orrhage (1962, 1974).

Head structure. 1–4. Prostomium. Distinct groove (Orrhage 1962: 430, figs 2–4).

5–9. Peristomium. Limited to lips (Orrhage 1962: 430, figs 2–4).

13–24. Palps. A peristomial pair of grooved palps is present (Orrhage 1962: 431).

25–28. Nuchal organs. The small lobe illustrated by Orrhage (1962: Textfigs 2–3) located between the bases of the palps, is here interpreted as a posterior lobe of the prostomium; the nuchal organs are located outside the palps on each side of this prolongation.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Orrhage 1974: figs 19–25).

31–43. First segment structure and appendages. First segments is similar with similar appendages to the rest of the body (Orrhage 1962: Textfigs 2, 3).

44–55. Parapodial structures. The structure of the noto- and neuropodia are very different. However, over the whole length of the body both rami are relatively well developed (Orrhage 1962: Textfig. 8) and are similar to those of other spiomorphs. Several segments carry notopodia with internal aciculae; most of these are flask-shaped with a distinct narrow distal end, considered here a unique form of dorsal cirrus, and ventral 'cirri' may be also present but are not considered homologous with other forms.

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are present (Orrhage 1962: Textfig. 8). Multiple pygidial cirri are present (Orrhage 1962: Textfigs 5–7).

Digestive system. 66–72. Stomodaeum. It can be argued that a simple axial pharynx is present, based on statements by Orrhage (1974: 12, 14, 16, fig. 3) describing the pharyngeal musculature. No form of pharyngeal organ is scored in Purschke & Tzetlin (1996: table 2) but their fig. 2D does not contradict statements made by Orrhage (1974).

84–88. Gular membrane and gut. Gular membrane is absent, and the gut is straight (Orrhage 1974).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present (Orrhage 1974: 20). Scored with '?' for the form since no illustrations are given and because of the problems over interpreting metanephromixia and mixonephridia (see Poecilochaetidae and Spionidae for this character).

96–99. Organisation/distribution of segmental organs. The anterior segmental organs in the first 12 segments are poorly developed (Orrhage

1974: 20). They appear to not be reproductive and hence excretory only. Gametes are found in the segments after 13 where well developed gonoducts are found (Orrhage 1974: 20–21).

100. Sperm morphology. No mitochondrial interpolation (Orrhage 1974: figs 39–40).

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Orrhage 1974: 10–11).

Chaetal structures. 105–124. Chaetae. Capillary chaetae are present.

Arenicolidae. General references: Ashworth (1904, 1912).

Head structure. 1–4. Prostomium. Distinct groove (Ashworth 1904: 215).

5–9. Peristomium. Limited to lips (Ashworth 1904: 217).

25–28. Nuchal organs. Present (Ashworth 1904: 220; Rullier 1951).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Storch 1968: fig. 22).

31–43. First segment structure and appendages. Similar to others but lacks appendages, though according to Ashworth (1904: 217–218), the first segment has chaetae in juveniles, but they are lost during development.

44–55. Parapodial structures. Tori are present (Ashworth 1904: 216).

56–59. Gills or branchiae. Parapodial gills are present (Ashworth 1904: 221).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are absent (Rullier 1951). Note that Ashworth (1904: 259) lists sensory organs without mentioning lateral organs.

Digestive system. 66–72. Stomodaeum. An axial simple proboscis is present (Ashworth 1904: pl. 1 figs 5–6; Dales 1962).

84–88. Gular membrane and gut. A gular membrane is present (Goodrich 1945: 189). The gut is a straight tube (Ashworth 1904: 234–237).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present (Goodrich 1900: 729–730; Ashworth 1904). Classified as mixonephridia, based on Goodrich (1900: 729–730; 1945) and Lillie (1906).

96–99. Organisation/distribution of segmental organs. A few pairs of segmental organs are present anteriorly, one pair being purely excretory (Goodrich 1945: 189, 206–209).

100. Sperm morphology. No mitochondrial interpolation (see Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Circulatory system is closed (Ashworth 1904: 239–244). Heart body is absent (Ashworth 1904: 243–245). The heart described by Dales & Cummings (1987) in *Arenicola marina* is not considered homologous with heart bodies.

Chaetal structures. 105–124. Chaetae. Are present in the form of capillaries and dentate hooks.

Capitellidae. General references: Eisig (1887); Hartman (1947).

Head structure. 1–4. Prostomium. Distinct groove (Eisig 1887: 12).

5–9. Peristomium. Limited to lips (Eisig 1887: pl. 2, figs 1, 5).

25–28. Nuchal organs. Present (Eisig 1887: 71, pls 7–8; Rullier 1951: 310).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Eisig 1887: pl. 14, fig. 11).

31–43. First segment structure and appendages. Eisig (1887: 11–12) referred to the first part of the body as the 'Kopfmundsegment'; this construction is here assumed to consist of the prostomium proper, called the 'Kopflapp' by Eisig, the peristomial remnants around the mouth and the first achaetigerous segment.

44–55. Parapodial structures. Though capillary chaetae are present in both rami in anterior chaetigers, tori are present in posterior chaetigers called 'Hakenwülste' Eisig (1887: 98–104).

56–59. Gills or branchiae. Absent. Some species have extensions from the body that may have a respiratory function. However, since there is no circulatory system, these extensions contain cavities from the coelomic cavity and are thus are not branchiae.

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are present (Eisig 1887: 76, pl. 2; Rullier 1951).

Digestive system. 66–72. Stomodaeum. A simple axial proboscis is present (Eisig 1887: 37, pl. 2, figs 1, 5; Dales 1962).

84–88. Gular membrane and gut. Gular membrane between segments 4 and 5 (Eisig 1887: 37, pl. 16, fig. 8). Gut is straight.

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia (Eisig 1887: 111–132; Goodrich 1945: 194). Nephromixia are absent since excretory and coelomoduct systems are usually separate, and only in a few taxa is there any fusion at all (Goodrich 1900,1945: 197).

96–99. Organisation/distribution of segmental organs. The excretory and gonoduct system can be restricted, e.g. in *Capitella*, but not in any way that can be considered homologous with other taxa (Goodrich 1945: 194–197). In other capitellids, e.g. *Dasybranchus*, the gametes and gonoducts extend along the posterior body. Given their own state in multistate coding.

100. Sperm morphology. No interpolation of mitochondria (see Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Circulatory system absent (Eisig 1887: 154).

Chaetal structures. 105–124. Chaetae. In anterior chaetigers, the chaetae are generally capillaries, and, in posterior chaetigers, chaetae are hooded multidentate hooks.

Chaetopteridae. General references: Joyeux-Laffuie (1890); Barnes (1965); Gitay (1969).

Head structure. 1–4. Prostomium. Distinct groove (Barnes 1965: fig. 4E, as dorsal lip).

5–9. Peristomium. Limited to lips (Barnes 1965: fig. 5, as ventral lip).

10–12. Antennae. Absent. The so-called 'antennae' present in *Phyllochaetopterus* (Barnes 1965: fig. 4D) do not appear to be true antennae.

13–24. Palps. A pair of peristomial grooved palps is present (Barnes 1965; Orrhage 1966; Gitay 1969).

25–28. Nuchal organs. Present and similar to spiomorphs (Rullier 1951: 310); Orrhage (1966: 105, fig. 3) showed nerves to the nuchal organs.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Joyeux-Laffuie 1890: pl. 20).

31–43. First segment structure and appendages. First segment is similar to others but have notopodial appendages only (Gitay 1969).

44–55. Parapodial structures. Tori are present (Gitay 1969; fig. 2D).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs unknown. Others absent.

Digestive system. 78–83. Ventral pharynges and associated structures. Dales (1962: 417) stated that the stomodaeum was a simple tube "without vestige of a proboscis".

84–88. Gular membrane and gut. No gular membrane, gut is straight (Joyeux-Laffuie 1890: 307–311).

Excretory/reproductive system. 89–95. Nephridial structures. Joyeux-Laffuie (1890: 318–332) described the organ system in detail. Goodrich (1945) classified the chaetopterid nephridial system with spiomorphs, but the issue is open as to whether they are mixonephridia or metanephromixia.

96–99. Organisation/distribution of segmental organs. Anterior segmental organs are excretory, posterior ones are fertile (Joyeux-Laffuie 1890).

100. Sperm morphology. Mitochondria not interpolated (Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Joyeux-Laffuie 1890: 311–316; Hanson 1949).

Chaetal structures. 105–124. Chaetae. Capillary spines in one anterior chaetiger and uncini are present.

Chrysopetalidae. General references: Perkins (1985); Watson Russell (1986,1989); Dahlgren & Pleijel (1995).

Head structure. 1–4. Prostomium. Distinct groove (Watson Russell 1986, fig. 2).

5–9. Peristomium. Limited to lips (Watson Russell 1986, figs 3–6).

10–12. Antennae. Both a median and pair of lateral antennae are present (Perkins 1985: 859, fig. 1c; Watson Russell 1986: fig. 2).

13–24. Palps. Present ventrally and tapering without articulation (Perkins 1985: 859, fig. 1d; Watson Russell 1986: fig. 3).

25–28. Nuchal organs. Present (Racovitza 1896: pl. 3, fig. 27).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. Jorge (1954: figs 1, 2) showed the prostomium as completely fused to the rest of the body but Watson Russell (1986: fig. 2) shows the head distinct from the first segment, but surrounded by it. The parapodia of the first segment are similar to those in other segments. Perkins (1985: 859) did not recognise the dorsal and ventral cirri of the first segment as tentacular cirri. However, Watson Russell (1986: figs 2–3; 1991: 286) identified them as tentacular cirri, and this is accepted here.

44–55. Parapodial structures. With expanded notopodial ridges (Watson Russell 1991: fig. 3A). Dorsal and ventral cirriform cirri are both present.

60–65. Sensory structures, papillae and pygidial cirri. A single pair of pygidial cirri (Uschakov 1955: 166).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. (Dales 1962: fig. 8A; Perkins 1985: 859; Watson Russell 1986: 156, fig. 10). A pair of lateral jaws is present (Perkins 1985: 859; Glasby 1993).

84–88. Gular membrane and gut. Gut a straight tube (Dahlgren pers. commun.).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia by Goodrich (1945: 187) based on Fage (1906) but also possibly metanephromixia (Goodrich 1945: 295). The latter hypothesis is accepted here, based on Fage (1906: fig. 41). Glasby (1993) regarded the position as unresolved and further investigation is

admittedly required. Ciliophagocytal organs were not mentioned by Goodrich (1945).

96–99. Organisation/distribution of segmental organs. Unknown.

100. Sperm morphology. No mitochondrial interpolation (Rouse & Dahlgren, in prep.).

Circulation. 101–104. Circulation and heart body. Closed circulation based on Ehlers (1864: 87) statement that it is easily tracked since the circulating blood is green. No heart body noted.

Chaetal structures. 105–124. Chaetae. Include aciculae, falcate compounds with one ligament, and capillaries.

Cirratulidae. General references: Caullery & Mesnil (1898); Day (1967); Blake (1991).

Head structure. 1–4. Prostomium. Distinct groove (Caullery & Mesnil 1898).

5–9. Peristomium. Limited to lips. Caullery & Mesnil (1898: 12) referred to the first visible ring (actually only half of one in most taxa because of the overlapping region of the prostomium), as an achaetigerous segment. This is accepted here as the first true segment; the lips then represent the peristomium.

10–12. Antennae. All anterior appendages (other than palps) are absent (Caullery & Mesnil 1898: 12).

13–24. Palps. A pair of peristomial grooved palps is present in some genera, such as *Chaetozone* and *Dodecaceria* (Caullery & Mesnil 1898: 13); in other taxa, this pair splits longitudinally during development and forms groups of longitudinally grooved 'tentacles'. It is assumed here that a pair is the plesiomorphic state.

25–28. Nuchal organs. Present (Caullery & Mesnil 1898: 12; Rullier 1951: 310).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Caullery & Mesnil 1898: pl. 5, fig. 5).

31–43. First segment structure and appendages. The first segment is similar to the next segments, despite forming only half of a segment in some taxa (e.g. *Cirratulus*). It is more or less complete in the taxa with a single pair of palps, such as *Chaetozone* (Caullery & Mesnil 1898: 12–13, pl. 2). There are no appendages apart from branchiae.

44–55. Parapodial structures. Both rami are similar (Fauvel 1927: 89). Chaetae in both rami are usually similar (Caullery & Mesnil 1898). The long appendages present in many cirratulids dorsal to the notopodia are dorsal branchiae, rather than notopodial cirri (Caullery & Mesnil 1898: 13–14 for *Dodecaceria*; see also Fauvel 1927: 89).

56–59. Gills or branchiae. See above.

60–65. Sensory structures, papillae and pygidial cirri. Pygidial cirri coded as absent (Uschakov 1955: 295) but see also Caullery & Mesnil (1898: 12).

Digestive system. 78–83. Ventral pharynges and associated structures. An eversible buccal bulb (Caullery & Mesnil 1898: pl. 2, figs 7, 14; Dales 1962).

84–88. Gular membrane and gut. Gular membrane present (Meyer 1887; Goodrich 1945: fig. 46). Gut a straight tube (Meyer 1887).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia (Goodrich 1945: 192).

96–99. Organisation/distribution of segmental organs. A single anterior pair is nephridial; others more posteriorly function as gonoducts (Meyer 1887; Goodrich 1945: 192).

100. Sperm morphology. No mitochondrial interpolation (Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Closed circulation with heart body (Meyer 1887; Mesnil 1899; Picton 1899; Kennedy & Dales 1958).

Chaetal structures. 105–124. Chaetae. Capillaries and spines are present generally. The hooks are not considered homologous with other forms.

Cossuridae. General references: Fournier & Petersen (1991); Tzetlin (1994); Rouse & Tzetlin (1997).

Head structure. 1–4. Prostomium. Distinct groove (Fournier & Petersen 1991).

5–9. Peristomium. Forms a distinct ring. Previously confused as a segment (see Fournier & Petersen 1991: 70).

25–28. Nuchal organs. Present (Laubier 1963: 834, fig. 1a–b).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Tzetlin 1994).

31–43. First segment structure and appendages. First segment and appendages are similar to others (Fournier & Petersen 1991).

44–55. Parapodial structures. Parapodia have similar rami (Laubier 1963: 863, fig. 1; Fournier & Petersen 1991: 71–74). No other appendages.

56–59. Gills or branchiae. The single dorsal branchia (Fournier & Petersen 1991: 70–71) of cossurids is regarded as apomorphic and scored as a separate state in multistate coding.

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are absent (Rouse & Tzetlin pers. obs.). Three anal cirri according to

Uschakov (1955: 296). Also Fournier & Petersen (1991: 74) and Jones (1956: fig. 1f).

Digestive system. 66–72. Stomodaeum. Tzetlin (1994) described the buccal tentacles as non-muscularised non-motile structures attached dorsally in the roof of the mouth. They are everted by pulling back the lower lip, rather than the normal eversion process which would also involve intrinsic muscles. This is given a separate state in multistate coding.

84–88. Gular membrane and gut. Gular membrane absent (Tzetlin 1994). Gut a straight tube (Fournier & Petersen 1991: 73).

Excretory/reproductive system. Little is known about the nephridial/gonoduct system although the gametes are in the posterior region of the body (Tzetlin 1994; Rouse & Tzetlin 1997).

100. Sperm morphology. No interpolation of mitochondria (Rouse & Tzetlin 1997).

Circulation. 101–104. Circulation and heart body. Circulatory system closed based on the branchia containing two distinct blood vessels, so at the very least a circulatory system is present (Fournier & Petersen 1991). Heart body not observed.

Chaetal structures. 105–124. Chaetae. The only chaetal structures relevant to this data matrix are capillary.

Ctenodrilidae. General references: Monticelli (1910); Sokolow (1911); Wilfert (1973); Purschke (1988); Petersen & George (1991).

Head structure. 1–4. Prostomium. Distinct groove (Wilfert 1973: 335, fig. 1).

5–9. Peristomium. Limited to lips (Wilfert 1973: fig. 1).

25–28. Nuchal organs. Present (Wilfert 1973: 335, fig. 1; Gelder & Palmer 1976; Petersen & George 1991: fig. 6b).

Trunk structures. 29–30. Segmentation and muscle bands. The complete transverse sections shown by Sokolow (1911: figs 10, 12) and Monticelli (1910: figs 36–41) show no signs of longitudinal muscles although the muscles are clearly present in more detailed figures (e.g. Monticelli 1910: fig. 43). Muscle banding is coded as absent but requires further investigation.

31–43. First segment structure and appendages. First segment is similar to those following but lacks chaetae. It apparently contains the anterior pair of segmental organs (Monticelli 1910: figs 7, 11; Sokolow 1911: figs 1, 14).

44–55. Parapodial structures. Absent, chaetae simply project.

56–59. Gills or branchiae. Dorsal gills are present in some taxa (Petersen & George 1991) and this is assumed to be plesiomorphic based on outgroup considerations that place them near or within the Cirratulidae (see Mesnil & Caullery 1897).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are absent. See SEM micrographs in Petersen & George (1991).

Digestive system. 78–83. Ventral pharynges and associated structures. An eversible ventral buccal bulb is present (Wilfert 1973: figs 1 and 5; Purschke 1988).

84–88. Gular membrane and gut. Gular membrane absent based on drawings in Petersen & George (1991). Gut a straight tube based on drawings in Petersen & George (1991).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia assumed to be mixonephridia based on similarity with cirratulid organisation (Wilfert 1973: 340).

96–99. Organisation/distribution of segmental organs. A single pair of anterior excretory segmental organs are present and gametes exit though more posterior ducts (Mesnil & Caullery 1897).

100. Sperm morphology. No interpolation of mitochondria (Rouse 1997).

Circulation. 101–104. Circulation and heart body. Circulatory system closed with heart body (Monticelli 1910: fig. 11; Wilfert 1973: 339–340, fig. 7).

Chaetal structures. 105–124. Chaetae. The genera *Raphidrilus* and *Raricirrus* of the subfamily Raphidrilinae (Petersen & George 1991: 185–208) have capillary chaetae and dentate hooks are present.

Diurodrilidae. General references: Kristensen & Niilonen (1982); Westheide (1990); Kristensen & Eibye-Jacobsen (1995).

Head structure. 1–4. Prostomium. Distinct groove (Kristensen & Niilonen 1982: figs 7–10).

5–9. Peristomium. Forms a ring (Kristensen & Niilonen 1982: figs 7–10).

25–28. Nuchal organs. Unknown.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segment is similar to those of the rest of the body (Kristensen & Niilonen 1982: fig. 2).

60–65. Sensory structures, papillae and pygidial cirri. The 'toes' of diurodrilids (Kristensen & Niilonen 1982: fig. 17) are interpreted here as a pair of pygidial cirri.

Digestive system. 66–72. Stomodaeum. A ventral buccal organ is

present (Kristensen & Niilonen 1982; Westheide 1990; Purschke & Tzetlin 1996). Assumed here that it is eversible.

84–88. Gular membrane and gut. Gular membrane is absent; gut is straight (Kristensen & Niilonen 1982: fig. 2).

Excretory/reproductive system. 89–95. Nephridial structures. Protonephridia are present (Westheide 1990: 17) but gonoducts are unknown.

96–99. Organisation/distribution of segmental organs. Uncertain, segmental organs appear to be along the body, but gonoducts, if present, must be restricted.

100. Sperm morphology. No mitochondrial interpolation (Kristensen & Niilonen 1982; Kristensen & Eibye-Jacobsen 1995).

Circulation. 101–104. Circulation and heart body. Absent (Westheide 1990: 18).

Chaetal structures. 105–124. Chaetae. Absent.

Dorvilleidae. General references: Jumars (1974); Westheide (1985); Purschke (1987a); Eibye-Jacobsen & Kristensen (1994).

Head structure. 1–4. Prostomium. Distinct groove (Jumars 1974).

5–9. Peristomium. Forms two rings (Eibye-Jacobsen 1994).

10–12. Antennae. A median and pair of antennae is the plesiomorphic condition (Eibye-Jacobsen & Kristensen 1994).

13–24. Palps. Presence of ventro-lateral palps is the plesiomorphic condition (Eibye-Jacobsen & Kristensen 1994).

25–28. Nuchal organs. Present (Eibye-Jacobsen & Kristensen 1994: fig. 1; Rullier 1951: 310).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Clark 1962: fig. 26).

31–43. First segment structure and appendages. Plesiomorphic condition is for segment and appendages to be similar to the rest of the body (Eibye-Jacobsen & Kristensen 1994).

44–55. Parapodial structures. Plesiomorphic condition is to have parapodia with projecting neuropodia and cirriform dorsal and ventral cirri (Eibye-Jacobsen & Kristensen 1994).

56–59. Gills or branchiae. Plesiomorphic condition is absent (see Eibye-Jacobsen & Kristensen 1994).

60–65. Sensory structures, papillae and pygidial cirri. Dorsal cirrus organs are present in *Dorvillea* sp. (Hayashi & Yamane 1994). This is assumed to be plesiomorphic for the family based on the cladistic position of this genus in Eibye-Jacobsen & Kristensen (1994). A single pair of pygidial cirri is also assumed to be the plesiomorphic condition (Eibye-Jacobsen & Kristensen 1994).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral hypertrophied muscular pharynx is present with ctenognath jaws (Ehlers 1868: pl. 18; Dales 1962; Kielan-Jaworowska 1966: 39–40; Purschke 1987a; Eibye-Jacobsen & Kristensen 1994).

84–88. Gular membrane and gut. No evidence of a gular membrane.

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia, found in *Schistomeringos* and *Dorvillea* (Fage 1906: 349; Smith & Ruppert 1988) are the plesiomorphic state based on the cladistic analyses of Westheide (1985) and Eibye-Jacobsen & Kristensen (1994), though protonephridia are present in some derived taxa e.g. *Apodotrocha* and *Dinophilus* (Brandenburg 1970; Westheide & Riser 1983). Ciliophagocytal organs have not been reported and the degree of nephridial/coelomoduct fusion requires further investigation.

96–99. Organisation/distribution of segmental organs. Scored as being along the body based on Smith & Ruppert (1988: 249).

100. Sperm morphology. No interpolation of mitochondria (see Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. According to Smith & Ruppert (1988: table 14), the blood vascular system is absent in small species but these are derived taxa (Eibye-Jacobsen & Kristensen 1994). Plesiomorphic condition is assumed to be closed circulation with no heart body as in other eunicemorphs.

Chaetal structures. 105–124. Chaetae. Include aciculae, capillaries, and dentate compounds with two ligaments.

Eulepethidae. General references: Pettibone (1969,1986).

Head structure. 1–4. Prostomium. Distinct (Pettibone 1969: fig. 1a).

5–9. Peristomium. Forms lips only (Pettibone 1969: fig. 11e).

10–12. Antennae. Three prostomial antennae are present (Pettibone 1989: fig. 1a).

13–24. Palps. A pair of ventral palps is present (Pettibone 1969: fig. 11e).

25–28. Nuchal organs. Present (Pettibone 1969: fig. 1b).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. Surrounds the head with parapodia similar to the rest of the body (Pettibone 1969: fig. 1a). Tentacular cirri present (Pettibone 1969: fig. 1e).

44–55. Parapodial structures. Neuropodia project (Pettibone 1969: fig. 1f, j). Dorsal cirri present, cirriform and elytra (Pettibone 1969: 3). Ventral cirri cirriform (Pettibone 1969: fig. 2b).

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present, though one is much longer (Pettibone 1969: 3).

Digestive system. 73–77. Axial muscular pharynx jaws and other structures. Two pairs of jaws (Dales 1962; Pettibone 1969: 3, fig. 11c).

84–88. Gular membrane and gut. No gular membrane. Gut with side branches assumed based on Darboux (1899: 256).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia assumed based on Goodrich's (1945) review as a generalisation for all scaleworms. Other features unknown.

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Aciculae, capillary chaetae and spines are present (Pettibone 1969).

Eunicidae. General references: Ehlers (1868); Hartman (1944a).

Head structure. 1–4. Prostomium. Distinct groove (Ehlers 1868: pl. 15, figs 4, 16).

5–9. Peristomium. Forms two rings (Ehlers 1868: pl. 15, fig. 4, 16).

10–12. Antennae. Median and pair present (Ehlers 1868: pl. 15, fig. 4; Orrhage 1995).

13–24. Palps. The ventro-lateral pair of the traditional 'antennae' (Ehlers 1868: pl. 15, fig. 5) are here interpreted as palps (see Orrhage 1995).

25–28. Nuchal organs. Present (Rullier 1951: 309).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Ehlers 1868: pl. 15, fig. 9; Clark 1962: figs 22, 23).

31–43. First segment structure and appendages. First segment and appendages is similar to the rest of the body (Ehlers 1868).

44–55. Parapodial structures. Parapodia have projecting neuropodia and cirriform dorsal and ventral cirri (Ehlers 1868: fig. 31).

56–59. Gills or branchiae. Parapodial gills present (Ehlers 1868: pl. 15, fig. 31).

60–65. Sensory structures, papillae and pygidial cirri. Dorsal cirrus organs are present (Hayashi & Yamane 1994). A pair of pygidial cirri are present (Ehlers 1868: pl. 14, fig. 3).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral hypertrophied muscular pharynx is present with labidognath jaws (Ehlers 1868; Dales 1962; Kielan-Jaworowska 1966: 40–42).

84–88. Gular membrane and gut. Gular membrane absent (Fauchald pers. obs.). Gut a straight tube (Fauchald pers. obs.).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia (Goodrich 1945: 186).

96–99. Organisation/distribution of segmental organs. Along the body (Fage 1906: 349).

100. Sperm morphology. Not interpolated (see Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Blood vessels in Ehlers (1868: pl. 15, fig. 9). A heart body is absent (Fauchald pers. obs.).

Chaetal structures. 105–124. Chaetae. Include aciculae, capillaries, and dentate compounds with two ligaments.

Euphrosinidae. General references: Gustafson (1930); Kudenov (1993).

Head structure. 1–4. Prostomium. Distinct (Kudenov 1993: fig. 7b).

5–9. Peristomium. Limited to lips (Kudenov 1993; fig. 17d).

10–12. Antennae. Median and lateral antennae are present (Kudenov 1993: fig. 7b).

13–24. Palps. Externally reduced palp nerves run to ventro-lateral lips according to Gustafson (1930). Scored as 'unknown'.

25–28. Nuchal organs. Present (Gustafson 1930: 436).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Gustafson 1930: pl. 36, fig. 4).

31–43. First segment structure and appendages. Dorso-lateral around head with parapodia similar to those in the remainder of the body (Kudenov 1993: fig. 8a).

44–55. Parapodial structures. Parapodia form notopodial ridges (Gustafson 1930: 416, fig. 49). Cirriform dorsal and ventral cirri are present (Kudenov 1993: fig. 7c).

56–59. Gills or branchiae. Parapodial gills are present at the base of the notopodia (Kudenov 1993: fig. 7n).

60–65. Sensory structures, papillae and pygidial cirri. Pygidial cirri are present, one pair (Ehlers 1864).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral hypertrophied pharynx with a thickened, ridged cuticle is present (Gustafson 1930: pl. 36, fig. 4).

84–88. Gular membrane and gut. Gular membrane absent (see Gustafson 1930). Gut a straight tube (Gustafson 1930: pl. 36, fig. 1).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia (Gustafson 1930: pl. 36, fig. 5; Goodrich 1945: 187).

96–99. Organisation/distribution of segmental organs. Along the body (Ehlers 1864: 78).

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Gustafson 1930: 442).

Chaetal structures. 105–124. Chaetae. Have a calcareous component. Aciculae, capillary chaetae and spines are present.

Fauveliopsidae. General references: McIntosh (1922); Hartman (1971); Riser (1987).

Head structure. 1–4. Prostomium. Distinct (Riser 1987: figs 7–8).

5–9. Peristomium. Limited to lips (Riser 1987: fig. 1).

3–24. Palps. A pair of peristomial grooved palps appear to be present based on descriptions by McIntosh (1922) and Hartman (1971).

25–28. Nuchal organs. Present (Riser 1987: 213, fig. 7).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segments and appendages is similar to those in the remainder of the body. There is no evidence that any anterior reduced segments are present (Fauchald 1972).

44–55. Parapodial structures. Parapodial rami are of similar size (Fauchald 1972: 221) with no cirri.

60–65. Sensory structures, papillae and pygidial cirri. Epidermal papillae are present. The inter-ramal papillae resemble the flabelligerid papillae in structure (Fauchald 1972: pl. 45, fig. c; Riser 1987: 213).

Digestive system. 78–83. Ventral pharynges and associated structures. Riser (1987: fig. 8) suggests that a ventral eversible buccal organ is present. A ventral buccal organ is scored as present by Purschke & Tzetlin (1996: table 2).

84–88. Gular membrane and gut. Gular membrane present, called a septum by Riser (1987: fig. 8). Riser (1987: 213) mentioned that the oesophagus is looped when the prostomium is retracted, but otherwise little is known.

Excretory/reproductive system. All unknown.

Circulation. 101–104. Circulation and heart body. Assumed closed based on Riser (1987: 213, fig. 11). Heart body unknown.

Chaetal structures. 105–124. Chaetae. Capillary chaetae are present.

Flabelligeridae. General references: Schlieper (1927); Spies (1973, 1975).

Head structure. 1–4. Prostomium. Spies (1975: 188) stated that the prostomium of the flabelligerids consisted of the prostomial lobe with four eyes, nuchal organs, dorsal lip and the palps; in a more restricted definition used here, the prostomium consists only of the prostomial lobe proper; the other organs are here considered either peristomial (upper lip) or emerging from the juncture of pro- and peristomium.

5–9. Peristomium. Limited to lips (see previous comment).

13–24. Palps. The pair of grooved palps are located at the junction between pro- and peristomium and are peristomial in origin. (Mesnil 1899: 81; Schlieper 1927: 339; Spies 1975: 189).

25–28. Nuchal organs. Present (Schlieper 1927: 377; Rullier 1951: 309, but see also p. 310; and also Spies 1975: 188–189).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Schlieper 1927: fig. 28; Storch 1968: fig. 29).

31–43. First segment structure and appendages. First segment is similar to those following and has basically similar appendages.

44–55. Parapodial structures. Parapodial rami are similar (Schlieper 1927: 333, figs 5–6).

56–59. Gills or branchiae. Spies (1973; see especially pl. 7, fig. 11) demonstrated that the branchial blood vessels emerge from the heart posterior to the emergence of the vessel covering the brain, suggesting a more posterior morphological position; assumed here that this is segmental, based on previous arguments above for the prostomium and peristomium. Thus, they are dorsal segmental branchiae.

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs were not mentioned in Rullier (1951) or Schlieper (1927). Jeener (1928) does list the flabelligerids among taxa with lateral organs; possibly no examinations have been made. Epidermal papillae are present (Mesnil 1899; Schlieper 1927: 341–342, fig. 13).

Digestive system. 78–83. Ventral pharynges and associated structures. An eversible ventral buccal organ is present (Spies 1975: pl. 6, fig. 19; Dales 1977).

84–88. Gular membrane and gut. Gular membrane is present (Schlieper 1927: 352). Gut is looped (Schlieper 1927: 354–359: figs 29, 37).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia are present (Schlieper 1927: 369–373; Goodrich 1945: 188).

96–99. Organisation/distribution of segmental organs. A single anterior excretory pair with posterior gonads and gonoducts (Schlieper 1927: 377).

100. Sperm morphology. Not interpolated (Rouse, in press).

Circulation. 101–104. Circulation and heart body. Circulation closed with heart body (Mesnil 1899: 82; Picton 1899; Schlieper 1927: 354; Spies 1973).

Chaetal structures. 105–124. Chaetae. Capillary chaetae as well as hooked compounds with folds are present. The relatively thick, distally blunt chaetae present in many flabelligerids could suitably be called

spines; they do, however, have exactly the same apparently segmented structure characteristic of flabelligerid capillaries.

Glyceridae. General references: Ehlers (1868); Arwidsson (1899); Åkesson (1968).

Head structure. 1–4. Prostomium. Distinct groove (Ehlers 1868: pl. 24. fig. 2).

5–9. Peristomium. Limited to lips (Ehlers 1868: pl. 24. fig. 1).

10–12. Antennae. A pair of antennae is present (Ehlers 1864: pl. 24. fig. 2).

13–24. Palps. The ventral-most 'antennae' (Day 1967; Fauchald 1977) are here interpreted as a pair of ventral tapering palps, based on Binard & Jeener (1927). This view was, however, rejected by Åkesson (1968) who gave limited support to Hanström's (1928) argument that the 'precerebral cone' represents fused palps. The issue requires further investigation.

25–28. Nuchal organs. No reports, assumed to be absent.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Ehlers 1868: pl. 24, fig. 23; Clark 1962: fig. 18; Storch 1968: fig. 15).

31–43. First segment structure and appendages. First segment is similar to those following and bears similar appendages.

44–55. Parapodial structures. Parapodia have projecting neuropodia and cirriform dorsal and ventral cirri (Ehlers 1868: pl. 24, fig. 29).

56–59. Gills or branchiae. Absent, since there is no circulatory system.

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present (Uschakov 1955: 168; Day 1967: fig. 16.1m).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Jaws form a cross (Ehlers 1868: pl. 24: 8, 13; Dales 1962).

84–88. Gular membrane and gut. Gular membrane absent. Gut is a straight tube (Ehlers 1868: pl. 24: fig. 7).

Excretory/reproductive system. 89–95. Nephridial structures. Protonephridia as protonephromixia (Goodrich 1945: 160, 166). Ciliophagocytal organs are present (Goodrich 1899,1945: 200).

96–99. Organisation/distribution of segmental organs. In most segments along body except the extreme anterior and posterior ends (Goodrich 1945: 160).

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Absent (Smith & Ruppert 1988: 234).

Chaetal structures. 105–124. Chaetae. Capillary chaetae, aciculae, and tapering compounds with a single ligament are present.

Goniadidae. General references: Ehlers (1868); Arwidsson (1899); Fauvel (1923).

Head structure. 1–4. Prostomium. Distinct groove (Ehlers 1868: pl. 24. fig. 36).

5–9. Peristomium. Limited to lips (Ehlers 1868: pl. 24. fig. 1).

10–12. Antennae. A pair of lateral antennae is present (Ehlers 1864: pl. 24. fig. 36).

13–24. Palps. As for the Glyceridae, the ventral-most 'antennae' are here interpreted as a pair of ventral tapering palps, based on Binard & Jeener (1927).

25–28. Nuchal organs. No reports, assumed to be absent.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Ehlers 1868: pl. 24, fig. 39; Clark 1962: figs 19, 20; Storch 1968: 295).

31–43. First segment structure and appendages. First segment is similar to those following but has neuropodia only (Fauchald 1977).

44–55. Parapodial structures. Parapodia have projecting neuropodia and cirriform dorsal and ventral cirri (Ehlers 1868: pl. 24, fig. 39).

56–59. Gills or branchiae. Absent since there is no circulatory system.

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present (Uschakov 1955: 175).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Jaws form a circlet (Ehlers 1868: pl. 24: 36, 41; Dales 1962).

84–88. Gular membrane and gut. Unknown.

Excretory/reproductive system. 89–95. Nephridial structures. Protonephridia as protonephromixia (Goodrich 1945: 164). Ciliophagocytal organs are absent (Goodrich 1945: 164).

96–99. Organisation/distribution of segmental organs. Anterior sterile, Goodrich (1899: 453) clearly describes gonoducts only being present in the posterior region of *Goniada.*

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Absent (Smith & Ruppert 1988: 234).

Chaetal structures. 105–124. Chaetae. Capillary chaetae, aciculae, and tapering compounds with a single ligament are present.

Hartmaniellidae. General reference: Imajima (1977).

Head structure. 1–4. Prostomium. Distinct (Imajima 1977: 211, fig. 2).

5–9. Peristomium. Forms two rings (Imajima 1977: 211, figs 2a, b).

10–12. Antennae. Absent (Imajima 1977: fig. 2a and c).

13–24. Palps. Absent (Imajima 1977: fig. 2b).

25–28. Nuchal organs. Imajima (1977: 212) reported nuchal organs as absent but such organs are actually present as small ciliated pads under a very shallow peristomial fold (Fauchald pers. obs.).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. The first chaetiger is here interpreted as the first segment. It is possible that an achaetigerous segment is present anterior to what is here considered the first segment, but this will have to be demonstrated histologically.

44–55. Parapodial structures. Parapodia have projecting neuropodia. The notopodia are reduced to dorsal cirri with internal acicula (Imajima 1977: fig. 2h–k). Cirriform dorsal and ventral cirri are present.

56–59. Gills or branchiae. Imajima (1977) illustrated the median parapodia as slightly bifurcated; the lower part of this structure appear to be branchial in nature; similarly, in the same region a superior lobe of the neuropodia appear to be branchial. With reservations scored as dorsal gills.

60–65. Sensory structures, papillae and pygidial cirri. Dorsal cirrus organs. are unknown. Pygidial cirri are present (Imajima 1977: 213, fig. 2l).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral hypertrophied stomodaeum is scored by inference from Imajima (1977: 212). The jaws are prionognath, not labidognath as suggested by Orensanz (1990) (Fauchald pers. obs.).

84–88. Gular membrane and gut. Gular membrane unknown. Gut is simple and straight (Fauchald pers. obs.).

Excretory/reproductive system. Unknown.

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Include capillaries, aciculae, and tapering compounds with double ligaments.

Hesionidae. General references: Westheide (1967); Glasby (1993); Pleijel (1993).

Head structure. 1–4. Prostomium. Distinct groove (Pleijel 1993: fig. 2A).

5–9. Peristomium. Limited to lips (Glasby 1993; Pleijel 1993: fig. 2C).

10–12. Antennae. Median and lateral pair are present (Glasby 1993; Pleijel 1993: fig. 7A), though the former may be absent.

13–24. Palps. Ventral palps are present (Pleijel 1993: fig. 7A; Orrhage 1996).

25–28. Nuchal organs. Present (Pleijel 1993: fig. 2A).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Clark 1962: figs 12, 13; Westheide 1967: fig. 21; Storch 1968: figs 11, 12).

31–43. First segment structure and appendages. First segments are indistinct and have tentacular cirri only (see Pleijel 1993: 159, fig. 2D).

44–55. Parapodial structures. Parapodia have projecting neuropodia (Glasby 1993). Cirriform dorsal and ventral cirri are present (Pleijel 1993: fig. 4G).

60–65. Sensory structures, papillae and pygidial cirri. One pair of pygidial cirri is present (Uschakov 1955: 194; Day 1967: fig. 11).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Though jaws may be lacking they are coded as present since one pair of lateral jaws is found in some hesionids and it is here assumed to be plesiomorphic for the group (Marion & Bobretzky 1875: pls 6, 7; Dales 1962; Glasby 1993). Further investigation is required.

84–88. Gular membrane and gut. Gular membrane absent, based on Westheide (1967). Gut a straight tube, based on Westheide (1967).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as metanephromixa are assumed to be the plesiomorphic state though protonephridia are also found in some small taxa (Fage 1906; Goodrich 1945; Westheide 1986; see also Glasby 1993). Ciliophagocytal organs are often present (Goodrich 1898a,1945: 200; Fage 1906) and this is assumed to be plesiomorphic. Requires further investigation.

96–99. Organisation/distribution of segmental organs. Though restricted in certain taxa (see Westheide 1967), hesionids are coded as having segmental organs along the body, based on Fage (1906).

100. Sperm morphology. Not interpolated (see Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Closed circulation can be present (Goodrich 1898a: 185, figs 1, 2; Smith & Ruppert 1988: 260) or absent (Smith & Ruppert 1988: 234, 260) but until further data are available, a closed circulatory system is assumed to be plesiomorphic, based on arguments of Westheide (1986) (but see Discussion). Heart body is absent.

Chaetal structures. 105–124. Chaetae. Capillary chaetae, aciculae and tapering compounds with a single ligament are present.

Histriobdellidae. General references: Haswell (1900, 1914); Shearer (1910); Jamieson *et al.* (1985).

Head structure. 1–4. Prostomium. Distinct groove (Shearer 1910: pl. 17, figs 1, 7; Haswell 1914: 199).

5–9. Peristomium. Positionally the mouth and jaws appear located as in the eunicens, (Haswell 1900: figs 1–5), and they have been scored accordingly, but with only a single ring as in the Onuphidae.

10–12. Antennae. Median and pair present, called 'tentacles' by Haswell (1900: figs 1–5) and Shearer (1910: pl. 19, fig. 30).

13–24. Palps. Present, ventro-lateral. Referred to as 'tentacles' but are considered palpal after study by Orrhage (1995) on other eunicemorphs.

25–28. Nuchal organs. Present (Foettinger 1884: 454; Shearer 1910: 327–328). Absent in *Stratiodrilus* according to Haswell (1900).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Haswell 1914: pl. 12, figs 7, 8).

31–43. First segment structure and appendages. Both *Histriobdella* and *Stratiodrilus* have five body-segments, all of which are rather similar in size (Shearer 1910: pl. 17, figs 1, 7; Haswell 1914: 199).

44–55. Parapodial structures. Haswell (1914: 199–200) referred to the projections on the body as 'legs'; structurally, they do not resemble parapodia.

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral hypertrophied pharynx with prionognath jaws (Foettinger 1884: 462; Shearer 1910: 317–320, Textfig. 5; Haswell 1914: figs 1–5; Mesnil & Caullery 1922).

84–88. Gular membrane and gut. No gular membrane. Gut a straight tube (Shearer 1910: 314–316).

Excretory/reproductive system. 89–95. Nephridial structures. Protonephridia are separate from coelomoducts (Goodrich 1945: 214).

96–99. Organisation/distribution of segmental organs. The histriobdellid condition cannot be considered homologous with any other, and so they are given their own state in multistate coding.

100. Sperm morphology. No interpolation (Jamieson *et al.* 1985).

Circulation. 101–104. Circulation and heart body. Absent (Shearer 1910; see also Smith & Ruppert 1988).

Chaetal structures. 105–124. Chaetae. Absent.

Ichthyotomidae. General reference: Eisig (1906).

Head structure. 1–4. Prostomium. Fused but distinct (Eisig 1906: 3–6, figs 1–3).

5–9. Peristomium. Limited to lips (Eisig 1906: 3–6, figs 1–3). The 'Mundkegel' on which the mouth opens is here considered peristomial.

10–12. Antennae. Eisig (1906: fig. 3) shows three antennal structures that are considered here as lateral and median.

13–24. Palps. Eisig (1906: figs 4–5) shows the presence of rudimentary palps as ventral bulges, resembling ventral palps.

25–28. Nuchal organs. Present (Eisig 1906: 6, fig. 3). The 'Wimperorgan' is here considered a nuchal organ.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Eisig 1906: pl. 4, fig. 23, pl. 8 fig. 14b).

31–43. First segment structure and appendages. First segment and appendages is similar to those following (Eisig 1906: figs 3–4).

44–55. Parapodial structures. Parapodia have projecting neuropodia, and cirriform dorsal and ventral cirri (Eisig 1906: 10–12, fig. 8).

56–59. Gills or branchiae. Not noted.

60–65. Sensory structures, papillae and pygidial cirri. Largely unknown. One pair of pygidial cirri is present (Eisig 1906: 8–9, figs 6, 7).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. The pharynx is scored as axial and hypertrophied with a pair of lateral jaws (Eisig 1906: pl. 3, figs, 6, 13, 14) though further investigation is required.

84–88. Gular membrane and gut. No gular membrane. Gut is a simple tract. (Eisig 1906).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as metanephromixia Goodrich (1945: 295). Nothing in Eisig's description Eisig (1906: 136–138) suggests the presence of a ciliophagocytal organ.

96–99. Organisation/distribution of segmental organs. Coded as along the body based on Eisig (1906: 136–138).

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Circulatory system is limited (Eisig 1906: 139).

Chaetal structures. 105–124. Chaetae. Capillary chaetae, aciculae and tapering or dentate compounds with a single ligament are present.

Iospilidae. General references: Bergström (1914); Fauvel (1923); Day (1967).

Head structure. 1–4. Prostomium. Distinct groove (Fauvel 1923: fig. 72e).

5–9. Peristomium. Limited to lips (Fauvel 1923: figs 73a, b).

10–12. Antennae. No antennae (Fauvel 1923: fig. 72a).

13–24. Palps. A pair of ventral palps is present (Fauvel 1923: 194, fig. 73a).

25–28. Nuchal organs. Present (Rullier 1951: 309).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segment is indistinct and has tentacular cirri only.

44–55. Parapodial structures. Parapodia have projecting neuropodia with dorsal and ventral cirriform cirri (Day 1967: fig. 6.1h).

60–65. Sensory structures, papillae and pygidial cirri. Pygidial cirri are absent (Day 1967).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Jaws are coded as present though four species lack them, the remaining four (all *Phalacrophorus*) have lateral jaws (e.g. Greeff 1879: fig. 26).

84–88. Gular membrane and gut. Unknown.

Excretory/reproductive system. Unknown.

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Include aciculae and tapering compound chaetae with a single ligament.

Lacydaniidae. General references: Marion & Bobretzky (1875); Day (1967); Uschakov (1972).

Head structure. 1–4. Prostomium. Distinct groove (Marion & Bobretzky 1875: 57, pl. 8, fig. 17).

5–9. Peristomium. Limited to lips (Marion & Bobretzky 1875: 57, pl. 7, fig. 17a).

10–12. Antennae. One lateral pair present (Marion & Bobretzky 1875: 57).

13–24. Palps. Marion & Bobretzky (1875) reported the presence of pair of ventral palps; their illustrations suggest that these resemble those present in hesionids, nereidids and aphroditids.

25–28. Nuchal organs. Present (Marion & Bobretzky 1875: 58, figs 17, 17A; Rullier 1951: 309).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. The first segment is distinctly narrower than the following segment and carries a pair of tentacular cirri (Marion & Bobretzky 1875: 57, pl. 8 fig. 17). Some species lack tentacular cirri, but here, it is assumed that their presence is plesiomorphic.

44–55. Parapodial structures. The notopodia, while well developed, are consistently shorter than the neuropodia (Marion & Bobretzky 1875; Pleijel & Fauchald 1993). Dorsal and ventral cirri present. In most cases, the dorsal cirri are somewhat ovoid, rather than truly cirriform, but are certainly not elytroid or foliose.

60–65. Sensory structures, papillae and pygidial cirri. Two or more pairs of pygidial cirri are present (Marion & Bobretzky 1875: 59, pl. 7, fig. 17c).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Jaws are absent (Marion & Bobretzky 1875: 59–60, fig. 17). Marion & Bobretzky (1875: 59) referred to the muscular part of the eversible pharynx as a proventricle; this is certainly possible, but the structure as illustrated resembles the pharyngeal structures of the hesionids rather than those of the syllids.

84–88. Gular membrane and gut. No gular membrane apparent, gut straight (Marion & Bobretzky 1875: fig. 17).

Excretory/reproductive system. Unknown.

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Aciculae, tapering compounds with a single ligament and capillaries.

Longosomatidae. General references: Hartman (1944b); Borowski (1995).

Head structure. 1–4. Prostomium. Distinct groove (Hartman 1944b: pl. 27, fig. 2).

5–9. Peristomium. Assumed to be limited to lips based on similarities with spiomorphs, but see Borowski (1995).

13–24. Palps. A pair of grooved peristomial palps are present (Hartman 1957; Borowski 1995).

25–28. Nuchal organs. Present, prolongated (Uebelacker 1984: fig. 10–2; Borowski 1995).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segment is similar to those following, but lacks appendages (Borowski 1995).

44–55. Parapodial structures. Parapodia are spioniform (Hartman 1944b: pl. 27, fig. 8).

56–59. Gills or branchiae. Gills are dorsally placed and cylindrical (Hartman 1944b: pl. 27, fig. 1).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are unknown. Pygidial cirri are absent (Borowski 1995: fig. 1c).

Digestive system. 78–83. Ventral pharynges and associated structures. An eversible ventral buccal organ appears to be present (Hartman 1944b: 322).

84–88. Gular membrane and gut. Unknown.

Excretory/reproductive system. Unknown.

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Capillary chaetae are present.

Lopadorhynchidae. General references: Day (1967); Uschakov (1972).

Head structure. 1–4. Prostomium. Distinct (Claparède 1870: pl. 11, fig. 2).

5–9. Peristomium. Limited to lips (Day 1967: fig. 5.6).

10–12. Antennae. A pair of antennae only (Claparède 1870: pl. 11, figs 2; Day 1967: 156).

13–24. Palps. The ventral pair of what is traditionally called two pairs of frontal antennae are here considered palps. Further investigation is required.

25–28. Nuchal organs. Present as pits (Claparède 1870: pl. 11, figs 2, 2A; Greeff 1879: fig. 23; Rullier 1951: 310).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segment indistinct with tentacular cirri only (Day 1967: 136).

44–55. Parapodial structures. Day (1967: 136) referred to the parapodia as uniramous. The foliose dorsal cirri are here considered representing the notopodia as in the phyllodocids. Ventral cirri are also present.

60–65. Sensory structures, papillae and pygidial cirri. Pygidial cirri are present in some taxa e.g, *Pelagobia longicirrus* (see Greeff 1879: fig. 23) and this is assumed to be plesiomorphic.

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Scoring of the proboscis as this form is based on Dales (1962: 397). There may be two lateral jaws in *Pelagobia* (Uschakov 1972: 187), though they are absent in *P. longicirrus* (Greeff 1879: fig. 19). In other lopadorhynchids the pharynx is also unarmed.

Excretory/reproductive system. Unknown.

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Aciculae and tapering compounds with a single ligament present.

Lumbrineridae. General reference: Ehlers (1868).

Head structure. 1–4. Prostomium. Distinct groove (Ehlers 1868: pl. 17, fig. 7).

5–9. Peristomium. Forms two rings (Ehlers 1868: pl. 17, figs 2, 7).

10–12. Antennae. Median and lateral antennae are present in some taxa (e.g. Day 1967: fig. 17.14h; Fauchald 1977 as nuchal papillae), and this is assumed to be the plesiomorphic state.

13–24. Palps. Absent (Ehlers 1868: pl. 17, figs 7, 8).

25–28. Nuchal organs. Present (Rullier 1951: 309).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Clark 1962: fig. 25).

31–43. First segment structure and appendages. First segment is similar to the rest of the body and bears similar appendages (Ehlers 1868: pl. 17, fig. 7).

44–55. Parapodial structures. Parapodia with projecting neuropodia are present with limited dorsal cirri and no ventral cirri (Day 1967: fig. 17.14j).

56–59. Gills. Parapodial gills are present in *Ninoe* but absent in the other two genera. Scored as absent though further investigation is required.

60–65. Sensory structures, papillae and pygidial cirri. Dorsal cirrus organs are present (Hayashi & Yamane 1994). Pygidial cirri present (Fauvel 1923: 430–434).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral hypertrophied muscular pharynx is present with labidognath jaws (Ehlers 1868: pl. 17, figs, 1, 2, 11; Dales 1962; Kielan-Jaworowska 1966: 40–42).

84–88. Gular membrane and gut. Gular membrane absent, gut straight (Ehlers 1868: pl. 17, fig. 1).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia (Fage 1906; Goodrich 1945).

96–99. Organisation/distribution of segmental organs. Unknown.

100. Sperm morphology. Not interpolated (Rouse 1988).

Circulation. 101–104. Circulation and heart body. Unknown.

Chaetal structures. 105–124. Chaetae. Aciculae, dentate compounds with double ligaments and capillary chaetae are present.

Magelonidae. General references: McIntosh (1878); Orrhage (1966); Jones (1968); Wilson (1982).

Head structure. 1–4. Prostomium. Distinct (Jones 1968: 273, figs 1–2).

5–9. Peristomium. Jones (1968: 273, figs 1–2) referred to the whole anterior structure between the prostomium and the first chaetiger as the peristomium in the adults; in the larvae this structure contains provisional chaetae (Claparède 1864: pl. 10, figs 9–14, pl. 11, figs 1–2) and thus represents an achaetigerous segment in the adults.

13–24. Palps. Based on Orrhage (1966), it is considered here that the palps of magelonids are homologous with paired peristomial grooved

palps, but further study is required. They are given their own state in multistate coding due to their papillated nature.

25–28. Nuchal organs. Absent (Orrhage 1966: 111).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Jones 1968: fig. 8; Lanzavecchia *et al.* 1988: figs V3A, B).

34–47. First segments structure and appendages. Segments are similar but lack appendages (see comment on peristomium).

44–55. Parapodial structures. Parapodia are spioniform (Jones 1968: figs 3–6).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs present (Jones 1968: 276–278, fig. 3). One pair of pygidial cirri present (McIntosh 1915: 218).

Digestive system. 78–83. Ventral pharynges and associated structures. Ventral eversible buccal organ (Orrhage 1973).

84–88. Gular membrane and gut. Gular membrane absent, gut straight (Jones 1968).

Excretory/reproductive system. 89–95. Nephridial structures. Nephridial types unknown. Goodrich (1945) proposed similarities with spiomorphs with little justification.

96–99. Organisation/distribution of segmental organs. Gametes lie posteriorly along with apparent segmental organs in all segments according to McIntosh (1878,1911) similar to other spiomorphs.

100. Sperm morphology. Mitochondria not interpolated (Rouse 1997).

Circulation. 101–104. Circulation and heart body. Complete circulation with no heart body (Jones 1968; McIntosh 1878), though one is reportedly present in larvae (Picton 1899: 270–271).

Chaetal structures. 105–124. Chaetae. Capillary chaetae and hooded dentate hooks.

Maldanidae. General references: Pilgrim (1965, 1966a, b, 1977, 1978); Rouse (1990).

Head structure. 1–4. Prostomium. Fused but distinct (Pilgrim 1966a: 456–457, fig. 1c–d).

5–9. Peristomium. Lips only. The region to the right of the label *rsi* in Pilgrim's illustration is here taken to be the peristomium proper; it would also include the lateral portions of the head, lateral to the nuchal grooves (Pilgrim 1966a: fig. 2).

25–28. Nuchal organs. Present (Rullier 1951: 309; Pilgrim 1966a: fig. 1c).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Pilgrim 1978: fig. 3a).

31–43. First segment structure and appendages. First segment is similar to those following and has similar appendage (Rouse 1990).

44–55. Parapodial structures. Tori are present (Pilgrim 1977: 290, fig. 4D; Rouse 1990).

56–59. Gills or branchiae. Absent. However in two genera, *Branchioasychis* and *Johnstonia* the posterior segments carry vascularised, digitiform extensions from the body-wall (Fauvel 1927: 167). These may be apomorphic features for the genera.

60–65. Sensory structures, papillae and pygidial cirri. Multiple cirri are present on the anal plaque of many species.

Digestive system. 66–72. Stomodaeum. Both a simple axial proboscis and ventral buccal organs occur within the family (Orrhage 1973; Dales 1977; Green 1994). Coded the group with '?' for these two characters (and eversibility of the ventral buccal organ)since the plesiomorphic condition in the family is unknown. In multistate coding they were given either state.

84–88. Gular membrane and gut. Gular membrane present (Pilgrim 1965: fig. 2, 1966a: fig. 2). Gut is straight (Pilgrim 1965: fig. 1).

Excretory/reproductive system. 89–95. Nephridial structures. Classified as mixonephridia by Goodrich (1945) with little apparent evidence. Pilgrim's (1978: fig. 2b) illustration most resembles a mixonephridium.

96–99. Organisation/distribution of segmental organs. Four anterior pairs in chaetigers 5–9 or 6–10 in two species of maldanid described to date. This resembles to situation found in arenicolids and they are coded with the same state, even though all are involved in reproduction.

100. Sperm morphology. No mitochondrial interpolation (Rouse & Jamieson 1987).

Circulation. 101–104. Circulation and heart body. Closed circulation and heart body absent (Pilgrim 1966b).

Chaetal structures. 105–124. Chaetae. Capillary chaetae and dentate hooks are present.

Myzostomidae. General references: Jägersten (1940); Grygier (1989).

Head structure. 1–4. Prostomium. Is fused and reduced (see Grygier 1989).

5–9. Peristomium. Assumed it is limited to the lips (see Jägersten 1940: fig. 6; Grygier 1989 in figures).

25–28. Nuchal organs. Unknown. Comparison of the lateral organs with nuchal organs (Eeckhaut & Jangoux 1993: 42) seems erroneous.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands difficult to determine due to occlusion of the coelom.

31–43. First segment structure and appendages. Jägersten (1940) gave

no evidence of an apodous or achaetous anterior segment; assumed here that the first chaetae belong to the first segment.

44–55. Parapodial structures. Parapodia are present with projecting neuropodia. Considered here that the marginal cirri found in many forms to be the remnants of notopodia and hence are dorsal cirri even if there can be many more than five pairs. Ventral cirri are present in many species but are often overlooked (see Grygier 1989: fig. 3A).

60–65. Sensory structures, papillae and pygidial cirri. Eeckhaut & Jangoux (1993: 42) reported that the myzostomid lateral organs, while similar to the nuchal organs of other polychaetes, were totally different from the structures called lateral organs among the polychaetes. Pygidial cirri are absent.

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Jaws are absent (Jägersten 1940: 14–15, 22–25).

84–88. Gular membrane and gut. Gular membrane absent, gut with side branches present (Jägersten 1940: 25–27; Eeckhaut *et al.* 1995).

Excretory/reproductive system. 89–95. Nephridial structures. Protonephridia are present and separate from any coelomoducts (Pietsch & Westheide 1987).

96–99. Organisation/distribution of segmental organs. The myzostome reproductive system is considered as a separate state in multistate coding (see Jägersten 1940; Pietsch & Westheide 1987).

100. Sperm morphology. No mitochondrial interpolation (Afzelius 1984).

Circulation. 101–104. Circulation and heart body. Absent (Smith & Ruppert 1988: 234).

Chaetal structures. 105–124. Chaetae. Capillary chaetae are present in larvae. Aciculae and falcate hooks are present in adults.

Nautiliniellidae. General references: Miura & Laubier (1989, 1990); Glasby (1993).

Head structure. 1–4. Prostomium. Fused but distinct (Glasby 1993: fig. 2A).

5–9. Peristomium. Limited to lips (Miura & Laubier 1989; Glasby 1993).

10–12. Antennae. One pair present. Glasby's (1993) interpretation is not accepted here and what he calls palps (Glasby 1993: fig. 2A) are coded here as as antennae. This is in agreement with structures called antennae in *Nautiliniella* (Miura & Laubier 1989); *Shinkai* (Miura & Laubier 1990: 320); *Petrecca* (Blake 1990: 681); and *Mytilidiphila* (Miura & Hashimoto 1993).

13–24. Palps. The peristomial cirri of Glasby (1993: fig. 2B) and postero-ventral antennae of Miura & Laubier (1990) are regarded here as palps. Further investigation is, however, required.

25–28. Nuchal organs. Unknown, 'not exposed' (Glasby 1993).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segment is similar to the following and has similar appendages (Glasby 1993).

44–55. Parapodial structures. Parapodia are biramous with poorly developed notopodia (Miura & Laubier 1989: 388, fig. 1e). Dorsal and ventral cirri are usually present.

60–65. Sensory structures, papillae and pygidial cirri. Dorsal cirrus organs appear to be present (see Glasby 1993: fig. 2A, 2C). Pygidial cirri are absent.

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Jaws are absent. Miura & Laubier (1989: 388) suggest that a proventricle was present, but this was rejected by Blake (1990: 682) and Glasby (1993). A proventricle is scored as present here but requires further investigation.

84–88. Gular membrane and gut. Unknown.

Excretory/reproductive system. Unknown.

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Aciculae present. The neuropodial 'spines' of Glasby (1993) are scored here as capillary chaetae since they do not resemble the spines seen in other taxa.

Nephtyidae. General references: Ehlers (1868); Fauvel (1923); Clark (1958); Paxton (1974).

Head structure. 1–4. Prostomium. Distinct (Ehlers 1868: pl. 23. fig. 6; Fauvel 1923: 364).

5–9. Peristomium. Lips only (Ehlers 1868: pl. 23. fig. 8; Paxton 1974: fig. 3).

10–12. Antennae. One pair present (Paxton 1974).

13–24. Palps. The nephtyids are normally characterised as having two pairs of antennae; one of which is lateral, the other is ventro-lateral and often, but not always, emerging posterior to the lateral antennae. Paxton (1974) pointed out the palp-like nature of the ventro-lateral antennae in some species, but the innervation of the two pairs of antennae (Clark 1958: 211–213, figs 5–7) does suggest that further investigation is required. Binard & Jeener (1928: 178) considered the ventro-lateral 'antennae' as homologous with ventral palps of nereidids and aphroditids.

25–28. Nuchal organs. Present (Rullier 1951: 309; Clark 1958: 213–214).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Ehlers 1868: pl. 23. fig. 22; Clark 1962: fig. 17; Storch 1968: fig. 14).

31–43. First segment structure and appendages. First segment is considered reduced but bears similar appendages to following segments, though the dorsal and ventral cirri are often enlarged (e.g. Ehlers 1868: pl. 23. fig. 6; Rainer 1984: figs 2a–b) and are here considered tentacular cirri.

44–55. Parapodial structures. Parapodial rami are similar in size (Ehlers 1868: pl. 23. fig. 5; Fauvel 1923: 364, fig. 142d–e).

56–59. Gills or branchiae. Are present but inter-ramal and not homologous with those of any other polychaete (see Clark 1956). Called interramal cirri in descriptive papers (e.g. Hartman 1950; Rainer 1984). Given a separate state in multistate coding.

60–65. Sensory structures, papillae and pygidial cirri. Hayashi & Yamane (1994: 769) reported that the nephtyids have organs similar to dorsal cirrus organs scattered over many areas, though they are not considered to be homologous. Pygidial cirri present, single pair.

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. A pair of lateral jaws present (Fauvel 1923: fig. 142c; Dales 1962: fig. 6).

84–88. Gular membrane and gut. Clark & Clark (1962) did not suggest that any anterior septum differed markedly from the other septa. Gut straight (Ehlers 1868: pl. 23. figs 24, 29, 30).

Excretory/reproductive system. 89–95. Nephridial structures. Protonephromixia and ciliophagocytal organs present (Goodrich 1945: 166, fig. 33).

96–99. Organisation/distribution of segmental organs. Along the body (Goodrich 1898a).

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Clark 1956).

Chaetal structures. 105–124. Chaetae. Aciculae and capillary chaetae are present.

Nereididae. General references: Ehlers (1868); Fitzhugh (1987); Glasby (1991,1993).

Head structure. 1–4. Prostomium. Distinct groove (Ehlers 1868: pl. 21).

5–9. Peristomium. Limited to lips (Ehlers 1868: pl. 19, fig. 2).

10–12. Antennae. One pair (Ehlers 1868: pl. 22) was found to be the plesiomorphic condition by Fitzhugh (1987).

13–24. Palps. Ventral palps present (Ehlers 1868: pl. 22; Orrhage 1993,1996).

25–28. Nuchal organs. Present (Racovitza 1896: 219, Textfig. 5, pl. 4, fig. 36; Rullier 1951: 309).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Clark 1962: figs 14–16; Storch 1968: fig. 10).

31–43. First segment structure and appendages. First segments indistinct or shortened with tentacular cirri only.

44–55. Parapodial structures. Though often of equal size, the results of Fitzhugh (1987) suggest that projecting neuropodia is the plesiomorphic condition in the family. Dorsal and ventral cirri are present.

56–59. Gills or branchiae. Fitzhugh (1987) found branchiae, when present in nereidids, to derived structures. The plesiomorphic condition is absent.

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present (Ehlers 1868: pl. 20, fig. 14).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. A pair of lateral jaws are present (Ehlers 1868; Dales 1962).

84–88. Gular membrane and gut. No gular membrane and a straight gut is present (Ehlers 1868: pl. 19, fig. 6).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present that are completely separate from ciliophagocytal organs (Goodrich 1945: 170–175).

96–99. Organisation/distribution of segmental organs. Along the body (Goodrich 1945: 170).

100. Sperm morphology. No interpolation of mitochondria (see Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Closed with no heart body (Ehlers 1868: pl. 18, figs 31–33).

Chaetal structures. 105–124. Chaetae. Aciculae and falcate compounds with single ligaments.

Nerillidae. General references: Goodrich (1912a); Purschke (1985); Westheide (1990).

Head structure. 1–4. Prostomium. Fused and distinct (Goodrich 1912a: figs 1–3).

5–9. Peristomium. Limited to lips (Goodrich 1912a: figs 1–3).

10–12. Antennae. Median and pair present (Goodrich 1912a: fig. 1).

13–24. Palps. Present ventro-laterally.

25–28. Nuchal organs. Present (Goodrich 1912a: figs 1, 2).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Goodrich 1912a: figs 22, 31).

31–43. First segment structure and appendages. First segment is similar to following but has a variability in terms of appendages from being biramous uniramous or lacking (Westheide 1990). The condition with the first segment the same as those following is considered here to be plesiomorphic, but further investigation is required.

44–55. Parapodial structures. Parapodial rami are similar (Goodrich 1912a: fig. 4; Westheide 1990). Nerillids are unusual among polychaetes in having inter-ramal cirri (Goodrich 1912a: fig. 4), but this is not relevant to the present analysis.

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is usually present (Westheide 1990).

Digestive system. 78–83. Ventral pharynges and associated structures. An eversible ventral buccal bulb is present with unique stylets (Purschke 1985).

84–88. Gular membrane and gut. Gular membrane is absent, gut is straight (Gelder & Uglow 1973).

Excretory/reproductive system. 89–95. Nephridial structures. Are difficult to assess based on Goodrich's (1945) criteria. Metanephridia are present in some species studied but others have protonephridia (Westheide 1990). Metanephridia are regarded as being the plesiomorphic condition. Some 'nephridia' have excretory functions in some segments and gonoduct functions in others. Coded as mixonephridia (rather than metanephromixia) until further studies are made.

96–99. Organisation/distribution of segmental organs. Along the body Westheide (1990).

100. Sperm morphology. Not interpolated (see Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Goodrich 1912a).

Chaetal structures. 105–124. Chaetae. Chaetal forms vary within the family. Some taxa (e.g. *Nerilla*) have capillary chaetae only. Other genera (e.g. *Mesonerilla, Micronerilla*) have tapering compounds with a single ligament (Westheide 1990). Compounds are coded as present, since it is likely that this is a plesiomorphic state for the group.

Oenonidae. General references: Ehlers (1868); Hartman (1944a).

Head structure. 1–4. Prostomium. Distinct groove (Ehlers 1868: pl. 17, figs 15, 25).

5–9. Peristomium. Forms two rings (Ehlers 1868: pl. 17, figs 15, 25).

10–12. Antennae. Median plus a pair of antennae are present in some taxa (e.g. Ehlers 1868: pl. 17, fig. 25), and this is assumed to be the plesiomorphic state.

13–24. Palps. Absent.

25–29. Nuchal organs. Present (Rullier 1951: 309–310).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Ehlers 1868: pl. 17, figs 21, 31).

31–43. First segment structure and appendages. First segment is similar to the rest of the body and bears similar appendages (Ehlers 1868: pl. 17, fig. 15, 25).

44–55. Parapodial structures. Parapodia with projecting neuropodia are present with limited dorsal cirri in some taxa and strap-like cirri in others (compare Day 1967: fig. 17.14e with Day 1967: fig. 17.18i). The limited condition is assumed to be plesiomorphic, but further investigation is required. No ventral cirri (Day 1967: fig. 17.14j).

60–65. Sensory structures, papillae and pygidial cirri. Dorsal cirrus organs are present (Hayashi & Yamane 1994). Usually, two pairs of pygidial cirri are present (Ehlers 1868: pl. 17, fig. 30).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral hypertrophied muscular pharynx is present with prionognath jaws (Ehlers 1868: pl. 17, fig. 19; Dales 1962; Kielan-Jaworowska 1966: 40–42).

84–88. Gular membrane and gut. Unknown.

Excretory/reproductive system. Unknown.

Circulation. 101–104. Circulation and heart body. Closed circulation, heart body unknown (see Ehlers 1868: pl. 17, fig. 31).

Chaetal structures. 105–124. Chaetae. Aciculae and capillary chaetae are present.

Onuphidae. General references: Ehlers (1868); Paxton (1979,1986).

Head structure. 1–4. Prostomium. Distinct groove (Ehlers 1868: pl. 13, figs 1, 2).

5–9. Peristomium. Forms a ring (Ehlers 1868: pl. 15, fig. 1; Paxton 1986; Eibye-Jacobsen 1994).

10–12. Antennae. Present (Ehlers 1868: pl. 15, fig. 4).

13–24. Palps. The most lateral pair of antennae (Ehlers 1868: pl. 13, fig. 5) are here interpreted as palps (see Orrhage 1995). The structures traditionally called frontal antennae (see Paxton 1986) are part of the buccal lips (Orrhage 1995) and are probably derived within the Onuphidae (see Paxton 1986: fig. 37).

25–28. Nuchal organs. Present (Rullier 1951: 309; Paxton 1986: fig. 5).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Ehlers 1868: pl. 13, fig. 4; Clark 1962: fig. 24; Paxton 1986: fig. 2).

31–43. First segment structure and appendages. Although those of the anterior body are somewhat different to those posterior (Paxton 1986), the first segments and appendages are basically similar to the rest of the body. The condition where they differ strongly from the other segments appears to be derived within the family (Paxton 1986: fig. 37).

44–55. Parapodial structures. Parapodia have projecting neuropodia and cirriform dorsal and ventral cirri (Paxton 1986: fig. 6).

56–59. Gills or branchiae. Parapodial gills present (Paxton 1986: fig. 7).

60–65. Sensory structures, papillae and pygidial cirri. Dorsal cirrus organs are present (Hayashi & Yamane 1994). A single pair of pygidial cirri is present in *Hyalinoecia* and other genera and is assumed to be the plesiomorphic condition (Ehlers 1868: pl. 13, fig. 3; Paxton 1986: 16).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral hypertrophied muscular pharynx is present with labidognath jaws (Ehlers 1868; Dales 1962; Kielan-Jaworowska 1966: 40–42).

84–88. Gular membrane and gut. Gular membrane absent (Fauchald pers. obs.). Gut a straight tube (Fauchald pers. obs.).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia (Goodrich 1945).

96–99. Organisation/distribution of segmental organs. Paxton (1979) described gametes in the middle third of the body in large onuphids. Hsieh & Simon (1991) described a similar result for females of *Kinberganuphis simoni*, but males had a much wider distribution of gametes. Onuphids are coded with either distribution along the body, or the anterior sterile condition.

100. Sperm morphology. Not interpolated (see Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Apparent dorsal and ventral blood vessels in Paxton (1986: fig. 2). Heart body is absent (Fauchald pers. obs.).

Chaetal structures. 105–124. Chaetae. Include aciculae, capillaries, and dentate compounds with two ligaments.

Opheliidae. General references: Brown (1938); McConnaughey & Fox (1949); Hartmann-Schröder (1958); Bellan *et al.* (1990).

Head structure. 1–4. Prostomium. Distinct groove (McConnaughey & Fox 1949: 320, fig. 1).

5–9. Peristomium. Limited to lips (McConnaughey & Fox 1949: 320, fig. 2).

25–28. Nuchal organs. Present (Brown 1938: figs 3, 7, 8; McConnaughey & Fox 1949: 320, fig. 1).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Brown 1938: fig. 9; McConnaughey & Fox 1949: fig. 20; Hartmann-Schröder 1958: fig. 70).

31–43. First segment structure and appendages. First segment is similar to those following and bears similar appendages (Brown 1938: fig. 3; McConnaughey & Fox 1949: fig. 1).

44–55. Parapodial structures. Parapodial rami are similar with no cirri (Brown 1938: figs 4, 11).

56–59. Gills or branchiae. Parapodial gills are present (Brown 1938: figs 4, 5; McConnaughey & Fox 1949: fig. 1).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are present (Rullier 1951; Hartmann-Schröder 1958: 108–109). Multiple pygidial cirri are present (Brown 1938: fig. 6).

Digestive system. 66–72. Stomodaeum. A simple axial proboscis is present (Brown 1938: figs 20–23; Dales 1962).

84–88. Gular membrane and gut. Gular membrane present and gut straight (Brown 1938: fig. 23; McConnaughey & Fox 1949).

Excretory/reproductive system. 89–95. Nephridial structures. Brown (1938: 154–155, fig. 26, 27) found metanephridia in *Ophelia cluthensis*. McConnaughey & Fox (1949: 323) reported protonephridia present in *Euzonus mucronata* (as *Thoracophelia*). Hartmann-Schröder (1958) described metanephridia in species of *Armandia*, *Ophelina*, *Ophelia*, *Polyapthalmus* and *Travisia*. She found protonephridia in *Euzonus furcifera*. *Euzonus* is a derived clade of the Opheliidae (Bellan *et al.* 1990), and the protonephridial condition is here considered secondary. Goodrich (1945: 189) classified opheliid segmental organs as mixonephridia, and, based on Brown (1938) and Hartmann-Schröder (1958), this is coded here.

96–99. Organisation/distribution of segmental organs. Brown (1938: 154–155) found three anterior pairs of segmental organs in *O. cluthensis*. McConnaughey & Fox (1949: 323) found segmental organs along the body but did not note any gonoducts. Hartmann-Schröder (1958) found considerable variability in the distribution of nephridial/coelomoduct system with taxa in *Polyophthalmus*, *Armandia*, and *Ophelia* having three to eight pairs usually in the mid-region of the body. Taxa such as *Travisia* and *Ophelina* had up to 27 pairs. The plesiomorphic state is difficult to determine at this time and the distribution of segmental organs is scored with '?' except where it was clearly absent.

100. Sperm morphology. Mitochondria not interpolated (Rouse 1988).

Circulation. 101–104. Circulation and heart body. Circulation is closed in all species examined. A heart body is present (Picton 1899; Brown 1938; McConnaughey & Fox 1949; Hartmann-Schröder 1958).

Chaetal structures. 105–124. Chaetae. Capillary chaetae are the only chaetae present that are relevant to this data set.

Orbiniidae. General references: Eisig (1914); Hartman (1957); Purschke (1988).

Head structure. 1–4. Prostomium. Distinct groove (Eisig 1914: pl. 11, fig. 1).

5–9. Peristomium. Forms a ring (Eisig 1914: pl. 19, figs 1, 8; Hartman 1957: 216, pl. 41, figs 1, 2).

25–28. Nuchal organs. Present (Eisig 1914: pl. 23, fig. 16; Rullier 1951: 310).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Eisig 1914: pl. 13, fig. 11).

31–43. First segment structure and appendages. Orbiniids have one or two anterior achaetous segments according to Solis-Weiss & Fauchald (1989). However, the peristomium forms a ring (Anderson 1959) and so the first segment is chaetigerous in orbiniins and achaetigerous in protoariciins (see Day 1977). It is assumed here that the first segments is same as rest as body and with similar appendages, i.e. the orbiniin state.

44–55. Parapodial structures. Parapodia have similar rami (see Eisig 1914: pl. 15), though some are similar to the spiomorph condition.

56–59. Gills or branchiae. Dorsal flattened gills are present (Eisig 1914: pl. 12).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are present (Eisig 1914: 396–398, pl. 21, figs 12, 15, 16). Dorsal organs are present (Hartman 1957: 219). Two to multiple pygidial cirri are present (Eisig 1914: pl. 23, figs 8, 20; Hartman 1957: pl. 22, fig. 2).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral eversible buccal bulb is present (Dales 1962: 419–420; Eisig 1914: pl. 11, figs 12, 14; Purschke 1988). The axial pharynx found in some orbiniids is derived from the ventral buccal bulb (Dales 1962: 419–420).

84–88. Gular membrane and gut. Gular membrane is absent, gut is straight, though a diverticulated anterior gut is present (Eisig 1914: 169–171, Textfig. 1).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia present as mixonephridia (Goodrich 1945: 185) but possibly metanephromixia (Goodrich 1945: 294). The group is therefore scored with '?' for these characters in A/P coding.

96–99. Organisation/distribution of segmental organs. In most segments of the body (Eisig 1914: 258).

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Closed circulation (Eisig 1914: pl. 13, fig. 11), heart body unknown.

Chaetal structures. 105–124. Chaetae. Aciculae, capillaries and spines are present.

Oweniidae. General references: Drasche (1885); Watson (1901); Wilson (1932); Dales (1957); Gardiner (1978).

Head structure. 1–4. Prostomium. Fused and reduced (Watson 1901: fig. 1).

5–9. Peristomium. Peristomium forms a ring (Watson 1901: fig. 1; Hartman 1965: pl. 44).

13–24. Palps. The palps (or crown) seen in oweniids appear to be prostomial (Dales 1957). The pair of palpal structures, as seen in *Myriowenia gosnoldi* (see Hartman 1965: pl. 44), is considered to be plesiomorphic based on outgroup considerations, and the 'crown' found in *Owenia fusiformis* is considered to be derived. Coded with prostomial palps.

25–28. Nuchal organs. Not noted by any authors (see Rullier 1951: 292), coded as absent (S. Gardiner pers. commun.).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present (McIntosh 1915: fig. 135).

31–43. First segment structure and appendages. First segment is similar to the rest of the body but has notochaetae only (as do several of the following segments) (Watson 1901; Hartman 1965: 208–209).

44–55. Parapodial structures. Tori are present (Watson 1901: fig. 20).

60–65. Sensory structures, papillae and pygidial cirri. Pygidial cirri, usually absent, are present in *Myriowenia gosnoldi* (Hartman 1965: pl. 44b).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral buccal organ homologous with those of other polychaetes is present but not used for feeding (Watson 1901; Dales 1957). It is eversible and used for tube building (Wilson 1932; Dales 1957). See also Purschke & Tzetlin (1996: fig. 10D).

84–88. Gular membrane and gut. No gular membrane, gut is a straight tube (Watson 1901; Dales 1957).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present (Gilson 1895). Goodrich (1945: 191) classified them as

mixonephridia, which is accepted here, though further investigation is required. No other evidence is available.

96–99. Organisation/distribution of segmental organs. Only one or two pairs of segmental organs are present in *Owenia*, in the fifth chaetiger (Gilson 1895). Gilson (1895) argued that these were responsible for gamete release. However, Watson (1901: fig. 20) clearly described spawning from the posterior region of the body though anal pores. This situation does not appear to be homologous with any other polychaete group, and they are coded with a separate state in multistate coding.

100. Sperm morphology. No mitochondrial interpolation (Rouse 1988).

Circulation. 101–104. Circulation and heart body. Circulation closed, heart body absent (Drasche 1885; S. Gardiner pers. commun.).

Chaetal structures. 105–124. Chaetae. Capillaries are present as well as dentate hooks (Hartman 1965: pl. 44).

Paralacydoniidae. General references: Fauvel (1914); Pettibone (1963).

Head structure. 1–4. Prostomium. Distinct groove (Fauvel 1914: pl. 7, fig. 2, 5).

5–9. Peristomium. Limited to lips (Fauvel 1914: pl. 7, fig. 2, 5).

10–12. Antennae. A pair of antennae are present (Fauvel 1914: pl. 7, figs 2, 5; Pettibone 1963: fig. 46a, b).

13–24. Palps. Normally characterised as having two pairs of antennae (Pettibone 1963: 185) interpreted here that the ventral pair are palps (see arguments under Nephtyidae, Phyllodocidae).

25–28. Nuchal organs. Unknown.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segment is reduced relative to those following. Pettibone (1963: fig. 46a) gives the impression of an achaetous first segment, but Fauvel (1914: figs 2, 5) shows a seemingly reduced first segment with appendages. Neuropodia only present (Pettibone 1963: 184–185). Tentacular cirri are absent.

44–55. Parapodial structures. Parapodia with projecting neuropodia, dorsal and ventral cirri present (Pettibone 1963: fig. 46c).

60–65. Sensory structures, papillae and pygidial cirri. Pygidial cirri are unknown (Pettibone 1963 suggests possibly absent).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Fauvel (1914: 121) suggests that the digestive apparatus is similar to that of lacydoniids and syllids. Pettibone (1963: 184) suggests that it is muscular, cylindrical and unarmed.

84–88. Gular membrane and gut. Unknown.

Excretory/reproductive system. Unknown.

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Aciculae, tapering compounds with a single ligament, and capillary chaetae are present.

Paraonidae. General references: Mesnil & Caullery (1898); Cerruti (1909); Hartman (1957); Strelzov (1979).

Head structure. 1–4. Prostomium. Is fused to the peristomium and distinct (Strelzov 1979; 5, fig. 1).

5–9. Peristomium. Strelzov (1979: 5–6, fig. 2) argues that the peristomium does not form a complete ring as postulated by Hartman (1957) and is limited to lips.

10–12. Antennae. A median antenna is present in paraonids that is apparently homologous with the other median antennae (Orrhage 1966; Strelzov 1979: 23).

13–24. Palps. Palpal evidence is present but not actual appendages that can be said to be homologous with grooved palps or ventral palps (see Orrhage 1966,1993). Scored with palps absent since further investigation is required on taxa that may have palpal innervation only.

25–28. Nuchal organs. Present (Cerruti 1909: fig. 2; Strelzov 1979: fig. 7).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Cerruti 1909; figs 18, 29).

31–43. First segment structure and appendages. First segment is similar to those following and has similar appendages. Strelzov (1979: 6) argued that an achaetous segment, as postulated by Hartman (1957), was an incorrect interpretation.

44–55. Parapodial structures. Parapodia have similar rami (Strelzov 1979: figs 23, 36).

56–59. Gills or branchiae. Present dorsal and flattened (Cerruti 1909: 474, figs 4, 7; Strelzov 1979: 17, fig. 5).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are present (Cerruti 1909: 482, figs 34, 37; Strelzov 1979: 24, fig. 25d). Three anal cirri are usually present (Strelzov 1979: 8–9).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral eversible buccal organ is present according to Strelzov (1979: 15–16), though Dales (1962: 414) observed a simple axial proboscis. Further investigation is required, but the view of Strelzov is adopted in the meantime.

84–88. Gular membrane and gut. A gular membrane is absent; the gut is straight (Strelzov 1979: 15–16).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present (Strelzov 1979: 18), but their organisation is too poorly known otherwise.

96–99. Organisation/distribution of segmental organs. Gamete distribution is in the posterior region of the body, and nephridia are present in the anterior segments. This appears to correspond most closely with the "anterior sterile condition", but there are conflicting descriptions about nephridial distribution (see Strelzov 1979: 18–19).100. Sperm morphology. Mitochondria not interpolated (Cerruti 1909: fig. 10).

Circulation. 101–104. Circulation and heart body. Circulation is closed; a heart body is absent (Strelzov 1979: fig. 17).

Chaetal structures. 105–124. Chaetae. Capillaries and hooded chaetae are present.

Parergodrilidae. General references: Karling (1958); Reisinger (1960); Purschke (1986, 1987b).

Head structure. 1–4. Prostomium. Fused and distinct (Reisinger 1960: fig. 14).

5–9. Peristomium. Forms a ring (Reisinger 1960: fig. 14).

25–28. Nuchal organs. Present in *Stygocapitella*, though absent in *Parerogodrilus* (Purschke 1986).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Karling 1958: 310, pl. 1c).

31–43. First segment structure and appendages. First segment similar to rest of body with similar appendages.

44–55. Parapodial structures. Absent. Chaetae simply project.

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral eversible buccal bulb present (Purschke 1987b).

84–88. Gular membrane and gut. Gut is straight, gular membrane absent, though possibly present in *Stygocapitella* (see Reisinger 1960: fig. 14).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present, but other details concerning nephromixia are not available.

96–99. Organisation/distribution of segmental organs. Nephridia are present along the body in *Stygocapitella*, though the gonoducts are restricted. In *Parerogodrilus*, they are restricted (Reisinger 1960). Requires further investigation.

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Reisinger 1960: fig. 14).

Chaetal structures. 105–124. Chaetae. Capillary chaetae are the only chaetae present relevant to this data set.

Pectinariidae. General references: Hessle (1917); Watson (1928); Holthe (1986a); Bartolomaeus (1995).

Head structure. 1–4. Prostomium. Fused to peristomium and reduced (Holthe 1986b: 17, fig. 2a–b).

5–9. Peristomium. Limited to lips. The peristomium is completely fused to the prostomium; it is assumed here to include the lips and the surrounding structures (Holthe 1986b: figs 2a, b, 3a, b).

13–24. Palps. The buccal tentacles, which cannot be retracted, are grooved and located on and around the lips (Holthe 1986b: fig. 2b) and are considered here peristomial palps. Early larval stages initially have a pair of these structures that are clearly similar to those seen in sabellariids (Watson 1928; fig. 4).

25–28. Nuchal organs. Present, similar to spiomorphs (Nilsson 1912; Rullier 1951: 309).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Storch 1968: 322–323).

31–43. First segment structure and appendages. First segment is completely fused to the head. The paleae are located on the first segment and are notopodial; the second and third segment usually carry only a pair of cirri each; segments 4 and 5 carry the branchiae. The first segment with normal notochaetae is segment 5 (Holthe 1986b: 19).

44–55. Parapodial structures. Tori are present (Bartolomaeus 1995: fig. 2).

56–59. Gills or branchiae. Dorsal lamellate gills are present on segments 4–5 (Holthe 1986).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are present (Rullier 1951: 309). Pygidial cirri are absent.

Digestive system. 78–83. Ventral pharynges and associated structures. First described by Watson (1928) as similar to that seen in terebellids. Dales (1963: 65) referred to the pectinariid structure as a ventral buccal organ used as a lip to sort food.

84–88. Gular membrane and gut. A gular membrane is present (Meyer 1887), and the gut is looped (Wirén 1885: 3–37; Brasil 1904: 105–100).

Excretory/reproductive system. 89–95. Nephridial structures. Goodrich (1945) listed the family among the terebellimorphs, hence with mixonephridia, but did not specifically mention any details of the nephridial

structures of this family. They are scored with mixonephridia here, though further investigation is required.

96–99. Organisation/distribution of segmental organs. Pectinariids have a few anterior pairs of segmental organs (Meyer 1887; Hessle 1917: 73–74).

100. Sperm morphology. Mitochondria not interpolated (Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Closed circulation with a heart body (Meyer 1887; Mesnil 1899; Picton 1899).

Chaetal structures. 105–124. Chaetae. Capillaries, spines in one anterior chaetiger, and uncini are present.

Pholoidae. General reference: (Pettibone 1992).

Head structure. 1–4. Prostomium. Distinct groove (Pettibone 1992: fig. 1B).

5–9. Peristomium. Limited to lips (Åkesson 1963: fig. 18; Pettibone 1992: 3).

10–12. Antennae. A median antenna and a pair are usually present (Pettibone 1992: fig. 1B).

13–24. Palps. Ventral palps are present (Åkesson 1963: fig. 18).

25–28. Nuchal organs. Unknown.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. While in *Pholoe minuta*, the first segments surround the head with tentacular cirri only (Åkesson 1963: 153, fig. 18), in some species, the first segment can have chaetae (see Pettibone 1992: figs 8–10) like following segments, and it is assumed here that this is the plesiomorphic condition.

44–55. Parapodial structures. Neuropodia project (Pettibone 1992: figs 1D, 1E). and elytra are present though dorsal cirri are absent. Ventral cirri present (Pettibone 1992).

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present (Pettibone 1992: 3).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Two pairs of jaws are present (Heffernan 1988: figs 2A–2C).

84–88. Gular membrane and gut. Gut a straight tube, gular membrane absent (Heffernan 1988).

89–95. Nephridial structures. Bartolomaeus & Ax (1992: 39–40, fig. 9.) show the development of metanephridia in *Pholoe minuta* and state that no mesodermal structures are involved. However, they did not discuss the morphology of mature individuals, and the possibility of there being mesodermal involvement is left open by coding '?' for the relevant characters.

96–99. Organisation/distribution of segmental organs. Anterior sterile. Gametes are found after segments 16 in *Pholoe minuta* Heffernan & Keegan (1988).

100. Sperm morphology. No mitochondrial interpolation (Heffernan & Keegan 1988).

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Aciculae and capillary chaetae are present. Compounds with a single ligament are present and are coded as dentate rather than falcate as termed by Pettibone (1992). They resemble those of sigalionids more than the falcate condition seen in, for example, sphaerodorids.

Phyllodocidae. General references: Bergström (1914); Pleijel (1991).

Head structure. 1–4. Prostomium. Distinct groove (Pleijel 1991: figs 4a, 7a, 9a).

5–9. Peristomium. Lips only (Pleijel 1991: fig. 11b).

10–12. Antennae. A pair of antennae is always present. A median antenna is present in plesiomorphic taxa (Pleijel 1991: 226).

13–24. Palps. The ventral-most 'antennae' (Fauchald 1977; Pleijel 1991) are here interpreted as a pair of ventral palps following Binard & Jeener (1929: 172).

25–28. Nuchal organs. Present (Rullier 1951: 309; Pleijel 1991: fig. 14A).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Clark 1962: fig. 7–10; Storch 1968; fig. 16).

31–43. First segment structure and appendages. First segment is indistinct and bears tentacular cirri only (Pleijel 1991: 227).

44–55. Parapodial structures. The presence of the foliose dorsal cirri is considered here to be evidence of the biramous nature of the parapodia; thus, in the terminology used here, all phyllodocids have biramous parapodia with projecting neuropodia and ventral cirri. The few taxa that have notopodial chaetae are plesiomorphic (Pleijel 1991: fig. 2).

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri are present (Pleijel 1991: figs 19b, 20c).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. The muscular axial pharynx has no jaws (Dales 1962: fig. 4A; Pleijel 1991: fig. 13C).

84–88. Gular membrane and gut. Gular membrane absent; gut is straight (Ehlers 1864: 138).

Excretory/reproductive system. 89–95. Nephridial structures. Protonephridia forming protonephromixia are present (Goodrich 1945: 155–158). Bartolomaeus (1989) argued that there was no mesodermal involvement in the formation of the funnel in *Anaitides mucosa*, but this is not relevant in the context of the coding since protonephromixia could be simply redefined to mean a combination of protonephridia and 'metanephridium' if Bartolomaeus's (1989) observation proves to be generally correct (see Discussion).

96–99. Organisation/distribution of segmental organs. Coded as along the body (Goodrich 1945: 155), though some anterior segments are not reproductive (Goodrich 1900).

100. Sperm morphology. No mitochondrial interpolation (Rouse 1988).

Circulation. 101–104. Circulation and heart body. According to Smith & Ruppert (1988: 233–234), the blood vascular system is reduced to main stems only.

Chaetal structures. 105–124. Chaetae. Aciculae, tapering compounds with a single ligament and capillary chaetae are present.

Pilargidae. General references: Fitzhugh & Wolf (1990); Licher & Westheide (1994).

Head structure. 1–4. Prostomium. Distinct groove (Fitzhugh & Wolf 1990: fig. 1).

5–9. Peristomium. Limited to lips (Pettibone 1966: fig. 4b). Glasby (1993) intepreted the peristomium as having two pairs of cirri, but this is regarded here as a cephalised segment.

10–12. Antennae. A median antenna and pair of antennae is considered the plesiomorphic condition by Licher & Westheide (1994). Fitzhugh & Wolf (1990) considered both alternatives. Further investigation is required, but pilargids are coded here as having a median and lateral pair of antennae.

13–24. Palps. Ventral palps considered present.

25–28. Nuchal organs. Nuchal organs have been lost within the Pilargidae but are present in plesiomorphic taxa (Fitzhugh & Wolf 1990; Licher & Westheide 1994).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segment is indistinct and has tentacular cirri only as the plesiomorphic condition (Fitzhugh & Wolf 1990; Licher & Westheide 1994).

44–55. Parapodial structures. Parapodia have projecting neuropodia with dorsal and ventral cirri as the plesiomorphic condition (Fitzhugh & Wolf 1990; Licher & Westheide 1994).

60–65. Sensory structures, papillae and pygidial cirri. Some pilargids have epidermal papillae, but this appears to be a derived condition within the clade (Fitzhugh & Wolf 1990). A single pair of pygidial cirri is present (Pettibone 1966: 160; Day 1967: 214), though, according to Uschakov (1955: 201), *Pilargis* lacks them.

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Muscular axial pharynx lacks jaws (Pettibone 1966: 160).

84–88. Gular membrane and gut. Unknown.

Excretory/reproductive system. Unknown.

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Aciculae and capillaries and notopodial spines are present.

Pisionidae. General references: Hartman (1939); Aiyar & Alikunhi (1940); Siewing (1953); Åkesson (1961); Stecher (1968).

Head structure. 1–4. Prostomium. Is small but distinct (Siewing 1953: fig. 1; Day 1967: fig. 4.1h; Stecher 1968: fig. 2).

5–9. Peristomium. Limited to lips (Siewing 1953: fig. 1A; Stecher 1968: fig. 2b).

10–12. Antennae. A pair of antennae are present in *Pisionidens indica* (Aiyar & Alikunhi 1940: fig. 1) but are absent in *Pisione remota* (Siewing 1953; Stecher 1968). *Pisionella hancocki* has a median antennae only (Hartman 1939). *Pisionidens indica* is regarded here as representing the plesiomorphic pisionid condition, but further investigation is required.

13–24. Palps. In *Pisione*, the palps are fused to first parapodium on the ventral side (Siewing 1953: fig. 1; Stecher 1968: fig. 2.). In *Pisionidens*, they emerge ventrally on the elongated, conical head structure (Aiyar & Alikunhi 1940: figs 1, 7c).

25–28. Nuchal organs. Absent in *Pisione* sp. (Rouse pers. obs.).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present (Aiyar & Alikunhi 1940: pl. 1, fig. 6; Stecher 1968: fig. 13c).

31–43. First segment structure and appendages. Surround and fused to head (Siewing 1953: 300; Stecher 1968: 353), but scoring is based on *Pisionidens* (Aiyar & Alikunhi 1940: 90, fig. 1) and hence scored as indistinct first segments with tentacular cirri only.

44–55. Parapodial structures. *Pisionidens* lacks chaetae except for aciculae as adults (Aiyar & Alikunhi 1940: 90, fig. 1) but have uniramous parapodia with compound chaetae and cirri as juveniles (Aiyar &

Alikunhi 1940: 90, fig. 8). The parapodia are interpreted here as having projecting neuropodia with cirriform dorsal and ventral cirri. Based also on comparisons with *Pisione* and *Pisionella* (Hartman 1939; Stecher 1968).

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present (Day 1967: 132).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Two pairs of jaws may be present dorsal and ventrally located (Hartman 1939; Aiyar & Alikunhi 1940: pl. 1, fig. 5; Stecher 1968: fig. 11). Homologies with the glycerid/goniadid condition should be investigated but coded here with the same state as scaleworms.

84–88. Gular membrane and gut. No gular membrane; gut is straight (Aiyar & Alikunhi 1940).

Excretory/reproductive system. 89–95. Nephridial structures. Protonephromixia are coded as present since Aiyar & Alikunhi (1940: 97) describe development of the genital funnels from mesodermal tissue in *Pisionidens indica*. Bartolomaeus & Ax (1992) argue that the ducts are nephridial (i.e. ectodermal) only in *Pisione* based on Stecher (1968). Further investigation is required (see section on Phyllodocidae and Discussion).

96–99. Organisation/distribution of segmental organs. Nephridia are present along the body, but the development of gonads and gonoducts is restricted, although in *Pisione remota*, females have eggs in up to 40 segments (Stecher 1968). Scored this taxon with a restricted distribution, though further investigation is required as to the plesiomorphic state in the group.

100. Sperm morphology. No mitochondrial interpolation (Westheide 1988).

Circulation. 101–104. Circulation and heart body. Circulatory system is absent (Smith & Ruppert 1988: 234).

Chaetal structures. 105–124. Chaetae. Aciculae, falcate compounds with a single ligament and capillary chaetae are present (see Parapodial character).

Poecilochaetidae. General references: Allen (1905); Orrhage (1964).

Head structure. 1–4. Prostomium. Distinct groove (Allen 1905: 86, fig. 7).

5–9. Peristomium. Limited to lips (Allen 1905: 86, fig. 7).

10–12. Antennae. Absent. The structure Allen (1905: 86) referred to as a median tentacle does not correspond to any of the categories of antennae enumerated here and appears to be an autapomorphy for the poecilochaetids.

13–24. Palps. A pair of peristomial palps is present (Allen 1905: fig. 7).

25–28. Nuchal organs. Present elongated (Allen 1905: 87, 111–114, fig. 7). The crest is detached along most of its length and usually divided into three separated, digitiform processes.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Allen 1905: figs 48, 49).

31–43. First segment structure and appendages. First segment projects forward but is basically similar to those following and has similar appendages (Allen 1905: 87, figs 1, 7, 8).

44–55. Parapodial structures. Parapodia are low ridges of the spiomorph type (Allen 1905: figs 9–11).

56–59. Gills or branchiae. Present, parapodial (Allen 1905: 91, fig. 11).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs present (Allen 1905: 100–111, fig. 2; Orrhage 1964). Multiple pygidial cirri are present (Allen 1905: 140: fig. 6).

Digestive system. 78–83. Ventral pharynges and associated structures. An eversible ventral buccal bulb is present (Allen 1905: 88, 115–116, fig. 42).

84–88. Gular membrane and gut. Gular membrane is absent, gut is straight (Allen 1905: 115–116).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present. Described as nephromixia by Allen (1905: 133). Goodrich (1945: 186) called them mixonephridia but suggested that they could also be metanephromixia (Goodrich 1945: 294). Further investigation is clearly required, and they are scored with '?' for both characters in A/P coding (see also Orrhage 1964).

96–99. Organisation/distribution of segmental organs. Anterior segmental organs are excretory only. Posterior ones act as gonoducts (Allen 1905: 133).

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Allen 1905: 126–141).

Chaetal structures. 105–124. Chaetae. Capillary chaetae, and spines are present in anterior and posterior chaetigers.

Poeobiidae. General references: Heath (1930); Pickford (1947); Robbins (1965).

Head structure. 1–4. Prostomium. Prostomium with distinct groove. Heath (1930: pl. 2, figs 5–6) and Robbins (1965: fig. 3a) show the prostomium everted. Robbins (1965: fig. 1) shows the body with the anterior end completely retracted.

5–9. Peristomium. Peristomium is distinct only as lips (Heath 1930: pl. 2, fig. 6).

13–24. Palps. A pair of grooved palps are present (Heath 1930: pl. 2, figs 5–6; Robbins 1965: figs 2b, 3a). Positionally, they appear similar to those present in the flabelligerids (Robbins 1965: 209) and have thus been scored as being peristomial rather than prostomial.

25–28. Nuchal organs. Present. (Robbins 1965: 209, fig. 5b).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

34–47. First segments structure and appendages. Poeobiids have two septa dividing the body into three coelomic pockets (Robbins 1965: fig. 1). The first one of these is no different from the other two externally.

44–55. Parapodial structures. Absent.

56–59. Gills or branchiae. The position of the branchiae corresponds closely to the position of the branchiae in the flabelligerids, and they have been scored as segmental dorsal branchiae. See illustrations in Heath (1930) and Robbins (1965) compared to illustrations in Spies (1973, 1975).

60–65. Sensory structures, papillae and pygidial cirri. Robbins (1965: 209, fig. 2b) describes papillae scattered over the gelatinous sheath.

Digestive system. 78–83. Ventral pharynges and associated structures. Ventral eversible buccal bulb present (Robbins 1965: 204–205, fig. 3a).

84–88. Gular membrane and gut. A gular membrane appears to be present (see Robbins 1965: fig. 1). The gut is looped.

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present. Their position suggests that they are mixonephridial as in flabelligerids, etc. (Robbins 1965: 203–204).

96–99. Organisation/distribution of segmental organs. One anterior pair of excretory segmental organs is present as well as a posterior pair of gonoducts (Robbins 1965: 207). Interpreted here that this is the same state as in cirratulids, acrocirrids and flabelligerids (among others).

100. Sperm morphology. No mitochondrial interpolation (Robbins 1965: 5d).

Circulation. 101–104. Circulation and heart body. Circulation is closed; a heart body is present (Pickford 1947: 290–297).

Chaetal structures. 105–124. Chaetae. Absent.

Polygordiidae. General references: Fraipont (1887); Salensky (1907); Westheide (1990).

Head structure. 1–4. Prostomium. Is fused to the peristomium but distinct (Fraipont 1887: pl. 3, fig. 1).

5–9. Peristomium. Forms a ring (Fraipont 1887: pl. 3, fig. 1.

13–24. Palps. Considered here that the palps of polygordiids are homologous with grooved palps, but they are given their own character 'prostomial paired', which is also seen in Protodrilidae, Protodriloididae and Saccocirridae. Further investigation is, however, required.

25–28. Nuchal organs. Present (Fraipont 1887: pl. 1, fig. 1; Westheide 1990: 13).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present (Fraipont 1887: pl. 5, figs 10–12).

31–43. First segment structure and appendages. First segment is similar to those of the rest of the body (Fraipont 1887: pl. 1, fig. 1).

44–55. Parapodial structures. Absent.

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri can be present (Fraipont 1887: pl. 2, fig. 3), and this is the assumed plesiomorphic state.

Digestive system. 66–72. Stomodaeum. A buccal organ is absent (Westheide 1990; Purschke & Tzetlin 1996).

84–88. Gular membrane and gut. Gular membrane is absent, and gut is straight (Fraipont 1887).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present, but there are no coelomoducts (Goodrich 1900, 1945: 224).

96–99. Organisation/distribution of segmental organs. Along the body (Westheide 1990: 14).

100. Sperm morphology. No mitochondrial interpolation (Franzén 1977).

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Westheide 1990).

Chaetal structures. 105–124. Chaetae. Absent.

Polynoidae. General references: Darboux (1899); Fauvel (1923); Pettibone (1963).

Head structure. 1–4. Prostomium. Distinct groove (Pettibone 1963: fig. 3b).

5–9. Peristomium. Limited to lips (Darboux 1899: fig. 15).

10–12. Antennae. A median antenna and a pair is usually present (Darboux 1899: fig. 22).

13–24. Palps. Ventral palps are present (Pettibone 1963: fig. 7a).

25–28. Nuchal organs. Present (Fauvel 1923: 84).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Darboux 1899: figs 8, 42; Clark 1962: figs 1, 2).

31–43. First segment structure and appendages. Surrounds the head

with parapodia reduced considerably compared with the rest of the body and two pairs of tentacular cirri (Pettibone 1963: fig. 3b). Coded this as a segment having tentacular cirri only.

44–55. Parapodial structures. Neuropodia project (Pettibone 1963: fig. 4g). Dorsal cirri cirriform and elytra (Pettibone 1963; figs 3a). Ventral cirri cirriform (Pettibone 1963: fig. 4k).

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present (Pettibone 1963: fig. 3a).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Two pairs of jaws (Darboux 1899: fig. 62; Dales 1962; Pettibone 1963: fig. 3c).

84–88. Gular membrane and gut. Gut side branches present (Darboux 1899: 218, fig. 73B).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia (Darboux 1899: 245–252; Goodrich 1945: 187). Ciliophagocytal organs are absent (Goodrich 1945).

96–99. Organisation/distribution of segmental organs. In most segments (Darboux 1899: 245–252; Goodrich 1945: 187).

100. Sperm morphology. No mitochondrial interpolation (Rouse 1988).

Circulation. 101–104. Circulation and heart body. Closed, a heart body is absent (Darboux 1899: 236–242; Hanson 1949).

Chaetal structures. 105–124. Chaetae. Aciculae and capillary chaetae and spines are present.

Pontodoridae. General references: Greeff (1879); Bergström (1914); Day (1967).

Head structure. 1–4. Prostomium. Distinct groove (Greeff 1879: fig. 19).

5–9. Peristomium. Not visible so assumed to be limited to lips (Greeff 1879: fig. 19; Day 1967: fig. 6.1B).

10–12. Antennae. Present pair only (Greeff 1879: fig. 19; Day 1967: fig. 6.1B).

13–24. Palps. A ventral pair is present (Greeff 1879: fig. 19; Day 1967: fig. 6.1B.

25–28. Nuchal organs. Present (Greeff 1879: 246, fig. 19).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segment is indistinct and has tentacular cirri only (Greeff 1879: fig. 19).

44–55. Parapodial structures. Day (1967: 167) referred to the parapodia as uniramous. The cirriform dorsal cirri are assumed to be notopodial. Ventral cirri are also present (Greeff 1879: fig. 20).

60–65. Sensory structures, papillae and pygidial cirri. Pygidial cirri present (Greeff 1879: fig. 22).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Jaws are absent, but a proventricle is present (Day 1967: 167; Greeff 1879: fig. 19).

84–88. Gular membrane and gut. Gut straight, no unusual septum mentioned by Greeff (1879: 247).

Excretory/reproductive system. Not enough information to score except for clearly absent features.

Circulation. No information.

Chaetal structures. 105–124. Chaetae. Capillaries, aciculae and tapering compounds with a single ligament are present.

Potamodrilidae. General references: Bunke (1967, 1988).

Head structure. 1–4. Prostomium. Fused but distinct (Bunke 1967: figs 78, 81a).

5–9. Peristomium. Lips only (Bunke 1967: 81a).

25–28. Nuchal organs. Although Bunke (1967: 339) clearly states that the 'Wimpergruben' (= nuchal organs) that are found in aeolosomatids are lacking in *Potamodrilus*, they would appear to be present (Bunke 1967: fig. 81b; 1988).

Trunk structures. 29–30. Segmentation and muscle bands. Segmentation present. Muscle banding appears to be present (Bunke 1967: figs 87–90).

31–43. First segment structure and appendages. All segments are similar with similar appendages (Bunke 1967: figs 78–80).

44–55. Parapodial structures. Considered absent here, and hence there are no associated appendages.

Digestive system. 78–83. Ventral pharynges and associated structures. A seemingly eversible ventral buccal bulb is present (Bunke 1967: fig. 81b).

84–88. Gular membrane and gut. Gular membrane absent, the gut is a straight tube (Bunke 1967,1988).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present, but any fusion with mesodermal components has not been documented (Bunke 1967: 346, fig. 91).

96–99. Organisation/distribution of segmental organs. The potamodrilids are hermaphrodites with nephridia in segments 1/2; female gonads in segment 5 and male gonads in segment 6. Apart from the features

associated with the hermaphroditic condition, this resembles most closely the restricted gonad region state (see Bunke 1967: 346–347, figs 86–82).

100. Sperm morphology. Mitochondria not interpolated (Bunke 1985).

Circulation. 101–104. Circulation and heart body. Circulation is closed, heart body is absent (Bunke 1967: 345–346).

Chaetal structures. 105–124. Chaetae. Are present and considered here as capillary forms, the only ones relevant to the characters here.

Protodrilidae. General references: Pierantoni (1908); Purschke & Jouin (1988); Westheide (1990); Nordheim & Schrader (1994).

Head structure. 1–4. Prostomium. Is fused to the peristomium but distinct (Pierantoni 1908: pl. 2).

5–9. Peristomium. Forms a ring (Pierantoni 1908: pl. 2).

13–24. Palps. Based on arguments presented by Purschke (1993), the palps of protodrilids are considered to be homologous with grooved palps, but they are given their own character 'prostomial paired', which is also seen in Polygordiidae, Protodriloididae and Saccocirridae.25–28. Nuchal organs. Present (Pierantoni 1908: pl. 2; Purschke 1990).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present in certain regions of some taxa and are assumed here to be plesiomorphic (Pierantoni 1908: pl. 7).

31–43. First segment structure and appendages. First segment is similar to those of the rest of the body (Pierantoni 1908: pl. 2).

44–55. Parapodial structures. Absent.

60–65. Sensory structures, papillae and pygidial cirri. The lateral organs mentioned by Westheide (1990: 11) are assumed here not to be homologous with those in other taxa. A pair of pygidial cirri is present (Pierantoni 1908: pl. 2).

Digestive system. 66–72. Stomodaeum. An eversible ventral buccal organ is present (Pierantoni 1908: pl. 4; Purschke & Jouin 1988; Westheide 1990; Purschke & Tzetlin 1996).

84–88. Gular membrane and gut. Gular membrane is absent, gut is straight (Pierantoni 1908: pls 3, 4).

Excretory/reproductive system. 89–95. Nephridial structures. The situation is somewhat confused but recent work by Nordheim appears conclusive. Protonephridia are present and metanephridia have also been recorded, (Goodrich 1945: 216–223; Westheide 1990: 12; Nordheim & Schrader 1994). Metanephridia may be associated with coelomoducts in the reproductive segments (of males only), but this is yet to be resolved (Goodrich 1945: 222–223). Examination of fig. 61 in Goodrich (1945) illustrates the problem. However, Nordheim (1991) shows convincingly that protonephridia are separate from the gonoducts in males and that the latter probably should be regarded as coelomoducts only.

96–99. Organisation/distribution of segmental organs. The anterior and posterior segmental organs are excretory only (Goodrich 1945: 216–219, 222–223), with a small number of segments in the anterior regions having gonoducts (Nordheim 1991).

100. Sperm morphology. No mitochondrial interpolation (Nordheim 1989).

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Pierantoni 1908: pl. 3). The listing in Smith & Ruppert (1988: 234) of this family as having reduced circulation, based on unpublished observations by Nordheim, needs confirmation.

Chaetal structures. 105–124. Chaetae. Absent.

Protodriloididae. General references: Remane (1926); Jouin (1966); Purschke & Jouin (1988).

Head structure. 1–4. Prostomium. Is fused to the peristomium but distinct (Jouin 1966: fig. 1).

5–9. Peristomium. Forms a ring (Jouin 1966: fig. 1).

14–20. Grooved Palps. Based on arguments presented by Purschke (1993) the palps of protodriloidids are considered to be homologous with grooved palps, but they are given their own character 'prostomial paired', which is also seen in Polygordiidae, Protodrilidae and Saccocirridae.

25–28. Nuchal organs. Present (Purschke 1988: fig. 3).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Jouin 1966: fig. 5).

31–43. First segment structure and appendages. First segment is similar to those of the rest of the body and has similar appendages, assuming the presence of chaetae in *P. chaetifer* is plesiomorphic (Jouin 1966: fig. 1).

44–55. Parapodial structures. Absent, though chaetae can be present (Jouin 1966).

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present (Jouin 1966: fig. 2).

Digestive system. 66–72. Stomodaeum. A ventral buccal organ is present (Purschke & Jouin 1988; Westheide 1990; Purschke & Tzetlin 1996) and assumed here to be eversible.

84–88. Gular membrane and gut. Gular membrane is absent, and the gut is straight (Jouin 1966: fig. 1).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present (Jouin 1966: 149), but the organisation with respect to

the coelomoducts is unknown. This result perhaps should be investigated in light of the findings by Nordheim (1991).

96–99. Organisation/distribution of segmental organs. Anterior nephridia are excretory, and gametes begin around segment 20 (Jouin 1966: 144, 149–152).

100. Sperm morphology. No mitochondrial interpolation (Jouin 1978).

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Jouin 1966: 147–148, fig. 4).

Chaetal structures. 105–124. Chaetae. The plesiomorphic condition is thought to be the presence of dentate hooks, variously called sigmoid chaetae or uncini (Purschke & Jouin 1988; Westheide 1990).

Psammodrilidae. General references: Swedmark (1952, 1955, 1958); Kristensen & Nørrevang (1982); Westheide (1990).

Head structure. 1–4. Prostomium. Distinct groove (Kristensen & Nørrevang 1982: fig. 2).

5–9. Peristomium. Forms two rings based on the developmental study by Swedmark (1955: figs 19–21). See also (Kristensen & Nørrevang 1982: fig. 2; Swedmark 1955: fig. 12).

25–28. Nuchal organs. Appear to be present in one species, *P. balanglossoides,* (see Swedmark 1955: figs 1, 5) and absent in other species. Assumed here that this represents a loss.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle banding appears to be present (Swedmark 1955: 159, pl. 3, fig. 12).

31–43. First segment structure and appendages. First segment is similar to those following with similar appendages if it is accepted that the peristomium forms two rings.

44–55. Parapodial structures. Parapodia are present with tori (Swedmark 1955: fig. 11). In the 'thorax' notopodial aciculae support long, slender 'cirri' (these are considered to be notopodia rather than cirri); in the 'abdomen', the hooks are neuropodial in position as low tori (Swedmark 1955; Kristensen & Nørrevang 1982).

Digestive system. 66–72. Stomodaeum. The pharyngeal structure of psammodrilids does not appear to be homologous with any other system described to date, and they are given their own state in multistate coding.

84–88. Gular membrane and gut. A pair of diaphragms in the pharyngeal region might qualify as gular membranes (Swedmark 1955: fig. 12), but developmental evidence suggests that they are not homologous (see Westheide 1990: 18).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present, but further data are unavailable (Swedmark 1955: 168–174; Kristensen & Nørrevang 1982: 272).

96–99. Organisation/distribution of segmental organs. A single pair of nephridia are present, and gametes are found in the abdomen, though no trace of gonoducts has been found (Swedmark 1955: 168; Kristensen & Nørrevang 1982: 272). Psammodrilids are scored with the condition based on anterior excretory and posterior gonoducts, though this is not entirely satisfactory.

100. Sperm morphology. No mitochondrial interpolation occurs from the description by Swedmark (1955: 174).

Circulation. 101–104. Circulation and heart body. Absent (Swedmark 1955: 190).

Chaetal structures. 105–124. Chaetae. Aciculae and dentate hooks are present.

Questidae. General references: Hobson (1970); Giere & Riser (1981); Jamieson & Webb (1984).

Head structure. 1–4. Prostomium. Distinct (Giere & Riser 1981: figs 2–3).

5–9. Peristomium. Forms a ring (Giere & Riser 1981: figs 2–3; Jamieson & Webb 1984: figs 1–3). The first part of what Hobson (1970: 193) called a biannulate first segment is considered here to be peristomial.

25–28. Nuchal organs. Present, called posterior groove of prostomium by Jamieson & Webb (1984: fig. 3) (see also Giere & Riser 1981: 96).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. The first part of what Hobson (1970: 193) called a biannulate first segment is here considered peristomial; the second part is considered an achaetigerous first segment (see Jamieson & Webb 1984: figs 3, 5).

44–55. Parapodial structures. Rami are similar in size (Hobson 1970: fig. 1a; Jamieson & Webb 1984: figs 1–3).

56–59. Gills or branchiae. Dorsal simple gills are present at the posterior end of the body (Jamieson & Webb 1984: fig. 21).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are present (Jamieson & Webb 1984: 26, fig. 4). Several pairs of pygidial cirri are present in at least one species (Jamieson & Webb 1984; fig. 21).

Digestive system. 78–83. Ventral pharynges and associated structures. An eversible ventral buccal bulb is present (Giere & Riser 1981: figs 2a, 3; Jamieson & Webb 1984: fig. 12).

84–88. Gular membrane and gut. A gular membrane is absent, and the gut is a straight tube (Jamieson & Webb 1984; 28).

Excretory/reproductive system. 89–95. Nephridial structures. Mentioned as 'nephridia' in Giere & Riser (1981: 97) with no further details. Coded as unknown.

96–99. Organisation/distribution of segmental organs. The reproductive system of the Questidae appears to be apomorphic and not homologous with any other condition.

100. Sperm morphology. No interpolation of mitochondria (Jamieson & Webb 1984).

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Giere & Riser 1981: 97, fig. 3).

Chaetal structures. 105–124. Chaetae. Capillaries and dentate hooks are present.

Sabellariidae. General references: Meyer (1887,1888); Dales (1952); Eckelbarger (1978); Orrhage (1978); Kirtley (1994).

Head structure. 1–4. Prostomium. Fused and reduced (Dales 1952: 450; Orrhage 1978: 366).

5–9. Peristomium. Limited to lips. The peristomium is completely fused to the prostomium and in part covered laterally by the projecting first segment, the chaetae of which form part of the operculum. The other part is formed by the notochaetae of the second segment (Orrhage 1978: 365).

13–24. Palps. The pair of palps is located well lateral to the narrowly ridged prostomium and is thus considered peristomial (Meyer 1887: pl. 24, figs 7–9; Dales 1952: fig. 13; Orrhage 1978: 352–353; Kirtley 1994: fig. 1.2.1).

25–28. Nuchal organs. Present (Rullier 1951: 272–274; Orrhage 1978: 365–366).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present (see Dales 1952: fig. 14).

31–43. First segment structure and appendages. The first segment is fused to the head. The notochaetae of the first two segments form part of the operculum (Dales 1952: 451). This is contrary to the terminology of Orrhage (1978: figs 1a, 1c) who viewed the first segments as having neuropodia only.

44–55. Parapodial structures. Tori are present; chaetal inversion is present in the sense that the uncini are located in a notopodial position (Knight-Jones 1981; Fitzhugh 1989).

56–59. Gills or branchiae. Dorsal flattened gills are present (Kirtley 1994: fig. 1.2.1.

Digestive system. 66–72. Stomodaeum. A buccal organ is absent (see Dales 1952; fig. 13).

84–88. Gular membrane and gut. Gular membrane not figured in Meyer (1887). Gut straight, but strongly differentiated along the length (Fauchald pers. obs.).

Excretory/reproductive system. 89–95. Nephridial structures. Mixonephridia (Goodrich 1945: 193).

96–99. Organisation/distribution of segmental organs. An anterior excretory pair followed by posterior gonoducts (Meyer 1887: 723–733, pl. 24, figs 7, 9; Goodrich 1945: 193).

100. Sperm morphology. Mitochondria not interpolated.

Circulation. 101–104. Circulation and heart body. Closed circulation with a heart body (Meyer 1887: pl. 24, figs 7, 8; 1888: 576–578; Picton 1899).

Chaetal structures. 105–124. Chaetae. Capillaries, anterior spines and uncini are present.

Sabellidae. General references: Meyer (1887, 1888); Johansson (1927); Evenkamp (1931); Orrhage (1980); Fitzhugh (1989); Rouse & Fitzhugh (1994).

Head structure. 1–4. Prostomium. Fused and reduced, forming the branchial crown (Rouse & Fitzhugh 1994: 288–289).

5–9. Peristomium. Forms a ring and collar (Rouse & Fitzhugh 1994).

13–24. Palps. The radiolar crown is a prostomial structure and is homologous with grooved palps (Orrhage 1980: 154–155; Rouse & Fitzhugh 1994: 289).

25–28. Nuchal organs. Present (Orrhage 1980: 123).

Trunk structures. 29–30. Segmentation and muscle bands. Present (Evenkamp 1931: fig. 20; Clark 1962: fig. 30).

31–43. First segment structure and appendages. The first segment is similar to those following but has notopodia only (Fitzhugh 1989).

44–55. Parapodial structures. Tori are present.

Digestive system. 66–72. Stomodaeum. No buccal organ is present (Dales 1962).

84–88. Gular membrane and gut. A gular membrane is absent, the gut is straight (Meyer 1887: pl. 24, fig. 14).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia present as mixonephridia (Goodrich 1945: 193).

96–99. Organisation/distribution of segmental organs. An anterior excretory pair of segmental organs and posterior gonoducts (Meyer 1887; Goodrich 1945: 193, fig. 46).

100. Sperm morphology. No mitochondrial interpolation (Rouse 1992).

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Meyer 1887: pl. 24, figs 14–16).

Chaetal structures. 105–124. Chaetae. Chaetal inversion is present. Capillaries, dentate hooks and uncini are present.

Saccocirridae. General references: Fraipont (1887); Goodrich (1901); Brown (1981); Westheide (1990).

Head structure. 1–4. Prostomium. Distinct groove (Brown 1981: fig. 2d).

5–9. Peristomium. Forms a ring (Brown 1981: figs 2c, 2d, 3; Goodrich 1901: fig. 2).

13–24. Palps. Based on arguments presented by Purschke (1993) the palps of saccocirrids are considered to be homologous with grooved palps but they are given their own character 'prostomial paired' which is also seen in Polygordiidae, Protodrilidae, and Protodriloididae.

25–28. Nuchal organs. Present (Brown 1981: fig. 2e; Goodrich 1901: fig. 1; Purschke 1990).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Fraipont 1887: pl. 16, figs 4, 5).

31–43. First segment structure and appendages. Similar to the rest of the body and has similar appendages (Goodrich 1901: fig. 2).

44–55. Parapodial structures. Parapodia are present (Westheide 1990: 9) and uniramous (Goodrich 1901: figs 2, 9) and represented by their own state in multistate coding.

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present (Brown 1981: fig. 9a, c, e).

Digestive system. 78–83. Ventral pharynges and associated structures. A ventral buccal bulb is coded as present for the saccocirrids though it is not present in all taxa. The presence of such a structure is arguably plesiomorphic (see Purschke & Jouin 1988). Eversibility is implied in the description by Goodrich (1901: 415) and is shown in *Saccocirrus papillocercus*, though admittedly, this is a species lacking a buccal organ (Purschke & Tzetlin 1996: fig. 1c).

84–88. Gular membrane and gut. Gular membrane is absent, gut is straight (Goodrich 1901: 415, fig. 2).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present and called nephromixia by Westheide (1990: 10), but the issue is unresolved (Goodrich 1901: 420).

96–99. Organisation/distribution of segmental organs. Along the body (Westheide 1990: 10).

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Closed circulation without a heart body (Goodrich 1901: 415–416).

Chaetal structures. 105–124. Chaetae. Capillary chaetae are present.

Scalibregmatidae. General references: Ashworth (1902); Dehorne & Dehorne (1913).

Head structure. 1–4. Prostomium. Distinct groove (Ashworth 1902: 243: fig. 3).

5–9. Peristomium. Forms a ring (Ashworth 1902: fig. 2).

13–24. Palps. Palpal evidence is present but not actual appendages that can be said to be homologous with grooved palps or ventral palps (see Orrhage 1966,1993). Scored with palps absent since further investigation is required on taxa that may have palpal innervation only.

25–28. Nuchal organs. Present (Ashworth 1902: 269, figs 3, 15).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Ashworth 1902: fig. 16; Storch 1968: fig. 25).

31–43. First segment structure and appendages. First segment similar with similar appendages to those following (Ashworth 1902: fig. 1).

44–55. Parapodial structures. Parapodia with similar rami and no cirri (Ashworth 1902: fig. 7).

56–59. Gills or branchiae. Parapodial gills present (Ashworth 1902: fig. 4).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are present (Ashworth 1902: figs 4, 7). Multiple pygidial cirri are present (Ashworth 1902: fig. 6).

Digestive system. 66–72. Stomodaeum. Simple axial pharynx present (Ashworth 1902: 256, fig. 14; Dales 1962).

84–88. Gular membrane and gut. No gular membrane; gut is straight (Ashworth 1902: fig. 14).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia are present (Ashworth 1902: 280–283; Goodrich 1945: 189–190).

96–99. Organisation/distribution of segmental organs. Along the body (Ashworth 1902: fig. 14), though he believed the mixonephridia were not large enough to shed gametes.

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Closed circulation (Ashworth 1902: 259–262); a heart body is absent (Ashworth 1902: 262).

Chaetal structures. 105–124. Chaetae. Capillary chaetae are the only relevant form present and most taxa lack spines.

Serpulidae. General references: Meyer (1887,1888); Loye (1908); Johansson (1927); Orrhage (1980).

Head structure. 1–4. Prostomium. Fused and reduced, forming the branchial crown (Orrhage 1980; Rouse & Fitzhugh 1994: 288–289).

5–9. Peristomium. Forms a ring and collar (Rouse & Fitzhugh 1994).

13–24. Palps. The radiolar crown is a prostomial structure and is homologous with palps (Orrhage 1980: 154–155; Rouse & Fitzhugh 1994: 289).

25–28. Nuchal organs. Present (Orrhage 1980: 124).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present (Meyer 1887: pl. 26, figs 11–14; Loye 1908: 320).

31–43. First segment structure and appendages. The first segment is similar to those following but has notopodia only (Knight-Jones 1981).

44–55. Parapodial structures. Tori are present.

Digestive system. 66–72. Stomodaeum. No buccal organ is present (Meyer 1887: pl. 26, fig. 7; Dales 1962).

84–88. Gular membrane and gut. A gular membrane is absent; the gut is straight (Loye 1908).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia present as mixonephridia (Goodrich 1945: 193).

96–99. Organisation/distribution of segmental organs. An anterior excretory pair of segmental organs and posterior gonoducts (Haswell 1885; Goodrich 1945: 193, fig. 46).

100. Sperm morphology. No mitochondrial interpolation (Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (Haswell 1885).

Chaetal structures. 105–124. Chaetae. Chaetal inversion is present. Capillaries and uncini are present.

Sigalionidae. General references: Ehlers (1864); Darboux (1899).

Head structure. 1–4. Prostomium. Distinct groove (Ehlers 1864: pl. 4, fig. 5).

5–9. Peristomium. Limited to lips (Ehlers 1864: pl. 4, fig. 6).

10–12. Antennae. A median antenna and a pair is usually present (Ehlers 1864: pl. 4, figs 5, 6).

13–24. Palps. Ventral palps are present (Ehlers 1864: pl. 4, fig. 6).

25–28. Nuchal organs. Present (Pruvot & Racovitza 1895: 456).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Clark 1962: figs 5, 6; Storch 1968: fig. 7).

31–43. First segment structure and appendages. Surrounds the head with parapodia similar to the rest of the body and tentacular cirri (Ehlers 1864: pl. 4, figs 5, 6).

44–55. Parapodial structures. Neuropodia project (Ehlers 1864: pl. 5, fig. 2). Dorsal cirri, cirriform and elytra. Ventral cirri cirriform (Ehlers 1864: pl. 4, pl. 5, fig. 2).

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present (Ehlers 1864: pl. 5, fig. 1).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Two pairs of jaws (Darboux 1899: 200–215; Dales 1962; Pettibone 1963: 45).

84–88. Gular membrane and gut. Gut side branches present (Darboux 1899: fig. 73A).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia (Darboux 1899: 245–252; Goodrich 1945: 187).

96–99. Organisation/distribution of segmental organs. In most segments (Darboux 1899: 245–252; Goodrich 1945: 187).

100. Sperm morphology. No mitochondrial interpolation (Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Closed; a heart body is absent (Darboux 1899: 236–242).

Chaetal structures. 105–124. Chaetae. Aciculae, dentate compounds with a single ligament, and capillary chaetae are present.

Sphaerodoridae. General references: Ruderman (1911); Reimers (1933); Fauchald (1974).

1–4. Prostomium. Assumed here that the plesiomorphic state is a distinct groove (e.g. Fauchald 1974: fig. 2.2) rather than fused, though further investigation is required.

5–9. Peristomium. Limited to lips (Reimers 1933: 53, fig. 2).

10–12. Antennae. A median and pair of antennae are present. The median antenna is often located well behind the frontal margin (Reimers 1933: fig. 4; Fauchald 1974: fig. 2.2).

13–24. Palps. The lower pair of 'frontal antennae' (when present) appear to correspond to the palps of nephtyids, etc., but studies of innervation have yet to be performed.

25–28. Nuchal organs. Present (Ruderman 1911: fig. 2; Reimers 1933).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present (Ruderman 1911: fig. 40).

31–43. First segment structure and appendages. First segment is indistinct and has tentacular cirri only (Fauchald 1974: figs 2.2, 4.19).

44–55. Parapodial structures. Called uniramous by Fauchald (1974).

Interpreted here as having projecting neuropodia since ventral cirri are present. Dorsal cirri are absent but may be represented by the macrotubercles.

60–65. Sensory structures, papillae and pygidial cirri. The tubercules of sphaerodorids are not considered homologous with other epidermal papillae. A pair of pygidial cirri is present (Ruderman 1911: fig. 3).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Reimers (1933) mentioned that the eversible pharyngeal cavity was covered with cuticle, but did not find jaws present. Dales (1962) claimed the presence of jaw-like structures, based on Ruderman (1911). However, a rasp–like structure rather than a jaw structure appears to be present (see Ruderman 1911: 76–77, fig. 39 d). A proventricle does appear to be present and is scored as such here (Ruderman 1911: fig. 41).

84–88. Gular membrane and gut. A gular membrane is absent, and the gut is spiralled but essentially straight (Ruderman 1911: figs 36, 41; Reimers 1933: 95–96, figs 1–2).

Excretory/reproductive system. 89–95. Nephridial structures. Ruderman (1911: 36–47) described protonephridia. Reimers (1933: 169–174) denied that the structures that Ruderman described were nephridia but rather deeply suspended groups of cells and cell nuclei from the epidermis. This seems to be a correct interpretation. Reimers (1933: 74) also denied that nephridia were present, but this seems to have been a misinterpretation. Examination of figures in both papers (Ruderman 1911: figs 31, 46; Ruderman 1933: fig. 18) suggests that metanephridia are present, possibly as mixonephridia (suggested by Goodrich 1945: 294). Scoring left as '?' on the issue of fusion of metanephridia with mesodermal elements.

96–99. Organisation/distribution of segmental organs. Only three pairs of segmental organs in *Ephesia* (or one pair in *Sphaerodorum*) (Reimers 1933: 75) are present in sphaerodorids studied to date. Given restricted state based on this.

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Limited or absent. A circulatory system is absent in *Sphaerodorum* Reimers (1933: 95) and only represented by unconnected dorsal and ventral vessels in *Ephesia* (Ruderman 1911: 87–88).

Chaetal structures. 105–124. Chaetae. Aciculae, falcate compounds with a single ligament and capillaries are present.

Spintheridae. General references: Graff (1888); Hartman (1948); Manton (1967).

Head structure. 1–4. Prostomium. Distinct groove (Manton 1967: fig. 1a).

5–9. Peristomium. Limited to lips (Manton 1967: fig. 1b).

10–12. Antennae. A single median antennae is present, called median tentacle by Manton (Hartman 1948: 15; Manton 1967: 5, fig. 3).

25–28. Nuchal organs. Absent based on Racovitza (1896: pl. 3, figs 22–26).

Trunk structures. 29–30. Segmentation and muscle bands. Unknown.

31–43. First segment structure and appendages. First segment dorsal-lateral around the head as in amphinomids and euphrosinids (Hartman 1948: fig. 1a; Manton 1967: fig. 1a).

44–55. Parapodial structures. Parapodia have distinct notopodial ridges as in amphinomids and euphrosinids (Hartman 1948: fig. 1b; Manton 1967; figs 2a, b). Ventral cirri present in some forms.

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present (Uschakov 1955: 226).

Digestive system. 66–72. Stomodaeum. The description by Manton (1967: 9–10, figs 1b, 3a) cannot be considered homologous with any other polychaete condition, and so they are scored this with their own state in multistate coding.

84–88. Gular membrane and gut. Gular membrane absent, gut branches laterally (Manton 1967: figs 2a, 3b).

Excretory/reproductive system. Unknown. Graff (1888: 54–55) suggests that the only genital opening is behind the anus, but further information is clearly required since gametes are clearly found throughout the body cavity.

Circulation. 101–104. Circulation and heart body. Closed, no mention of heart body (Graff 1888: 49–51).

Chaetal structures. 105–124. Chaetae. The chaetae of spintherids appear to not have a calcareous component. Hartman (1948: 17) referred to the chaetae as yellow; Manton (1967: 7) described the staining properties, neither one of which is characteristic of calcified chaetae. Spines are present. Compound hooks (with a fold) are termed 'chaetae', and the finer slender tapering rods 'aciculae' in agreement with Hartman (1948: 17). Manton (1967: 2) reversed the usage.

Spionidae. General references: Söderström (1920); Orrhage (1964); Foster (1971).

Head structure. 1–4. Prostomium. Distinct groove Foster (1971: pl. 1).

5–9. Peristomium. Limited to lips, may surround peristomium somewhat (Foster 1971: 9, pl. 1).

10–12. Antennae. A median antenna is present (Orrhage 1964: 386) though it is absent in some taxa.

13–24. Palps. A pair of grooved peristomial palps is present (Orrhage 1964; Foster 1971: pl. 1).

25–28. Nuchal organs. Present, elongate (Söderström 1920: 101; Orrhage 1964: Textfig. 6).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Clark 1962: figs 27, 28; Orrhage 1964: pl. 12, fig. 5).

31–43. First segment structure and appendages. First segment is similar to those following and with similar appendages (Foster 1971: pl. 1).

44–55. Parapodial structures. Parapodia with spioniform morphology (see Foster 1971: pl. 2A). Foster (1971: 9–10) referred to the lamellar parapodial structures as notopodial and neuropodial lamellae. Fauvel (1927) used the term dorsal and ventral cirri about the same structures. Foster (1971) is followed. True dorsal and ventral cirri are absent.

56–59. Gills or branchiae. Present dorsal, flattened.

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs present, dorsal organs present (Orrhage 1964: 355–362, Textfigs 6, 7). Multiple pygidial cirri are present. The most common is a pattern in which there is a median ventral cirrus plus a varying numbers of lateral pairs (Mesnil 1896: 268; Foster 1971: 9), and this is assumed to be plesiomorphic.

Digestive system. 78–83. Ventral pharynges and associated structures. Orrhage (1964: 362–370) demonstrated a great variation in the development of the eversible pharyngeal organ after Dales (1962) had characterised it as a simple axial pharynx. In many cases, a ventral buccal bulb is present and so they are coded with '?' for these two characters and as either state in multistate coding.

84–88. Gular membrane and gut. A gular membrane is absent, and the gut is straight (see Orrhage 1964: Textfig. 8).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present (Goodrich 1945: 185, fig. 45). The issue of their status as metanephromixa or mixonephridia is unresolved (see Poecilochaetidae).

96–99. Organisation/distribution of segmental organs. Anterior excretory segmental organs are present followed by gonoducts (Orrhage 1964: 376–378).

100. Sperm morphology. No mitochondrial interpolation (see Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (implied) (Mesnil 1896: 263). Picton (1898: 270) reported a heart body in spionids, but no confirmation of this passing mention has been published.

Chaetal structures. 105–124. Chaetae. Capillary chaetae, dentate hooks and hoods are present.

Sternaspidae. General references: Vejdovsky (1882); Goodrich (1898b); Dahl (1955).

Head structure. 1–4. Prostomium. Distinct groove (Vejdovsky 1882: pl. 3, fig. 3; Goodrich 1898b: figs 15–16).

5–9. Peristomium. Limited to lips (Goodrich 1898b: figs 15–16).

13–24. Palps. A pair of peristomial palps may be present. Sluiter (1882) noted the presence of a pair of appendages that appear to be attached to the peristomium. Palps are coded as absent since they have not been noted in other *Sternaspis* species, and further investigation is required.

25–28. Nuchal organs. Absent (?). Despite a careful examination, Dahl (1955: 15) stated: "The cuticular papillae are the only sense organs hitherto encountered in *Sternaspis*". It is possible that the anteriorly located upper lip nerve represents a remnant of a nuchal organ.

Trunk structures. 29–30. Segmentation and muscle bands. Longitudinal muscles form many bands, not discrete bundles (Vejdovsky 1882: pl., fig. 4; Goodrich 1898b: fig. 19).

31–43. First segment structure and appendages. First segment is similar and bears similar appendages to those following (Vejdovsky 1882: pl. 1, fig. 1; Goodrich 1898b: fig. 16).

44–55. Parapodial structures. Parapodial rami are similar except in the posterior region (Goodrich 1898b: fig. 16). No cirri are present.

56–59. Gills or branchiae. Present dorsally (Goodrich 1898b; fig. 16).

60–65. Sensory structures, papillae and pygidial cirri. Papillae are present (Dahl 1955: 14–15).

Digestive system. 66–72. Stomodaeum. A simple axial pharynx is present (Goodrich 1898b: fig. 17).

84–88. Gular membrane and gut. No gular membrane; the gut looped and folded (Vejdovsky 1882: pl. 1, fig. 12; Goodrich 1898b: fig. 17).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia present as mixonephridia (Goodrich 1945: 188–189).

96–99. Organisation/distribution of segmental organs. An anterior excretory pair and pair of posterior gonoducts (Goodrich 1945: 188–189), similar to *Poeobius*.

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Circulation is closed, a heart body is absent (Vejdovsky 1882: 57–60).

Chaetal structures. 105–124. Chaetae. Capillaries and spines in anterior chaetigers are present.

Syllidae. General reference: Malaquin (1893).

Head structure. 1–4. Prostomium. Distinct groove (Malaquin 1893: pl. 2, fig. 9).

5–9. Peristomium. Limited to lips (Malaquin 1893: pl. 4, figs 1–5). Glasby (1993) intepreted the peristomium as having cirri, but this is regarded here as the first segment.

10–12. Antennae. A pair of antennae and a median antenna are present (Malaquin 1893: pl. 2, fig. 9).

13–24. Palps. Present ventrally (Malaquin 1893: pl. 2, fig. 9; Orrhage 1996).

25–28. Nuchal organs. Present (Malaquin 1893: 176–185).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present (Malaquin 1893: pl. 6, fig. 14).

31–43. First segment structure and appendages. First segment is similar to those following but bears tentacular cirri only (Malaquin 1893: pl. 2, fig. 1).

44–55. Parapodial structures. Neuropodia project, dorsal and ventral cirri present (Malaquin 1893: pl. 6, fig. 14).

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present. (Malaquin 1893: pl. 14).

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Jaws, when present, take the form of a median tooth (a separate state in multistate coding). The possibility that the tooth is homologous paragnaths should be investigated (see Purschke 1988). A proventricle is present (Malaquin 1893: pl. 4).

84–88. Gular membrane and gut. Gut is straight with no gular membrane (Malaquin 1893).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present as metanephromixia (Goodrich 1945: 178–185).

96–99. Organisation/distribution of segmental organs. Along the body (Goodrich 1945: fig. 41).

100. Sperm morphology. No mitochondrial interpolation (see Jamieson & Rouse 1989).

Circulation. 101–104. Circulation and heart body. Closed circulation with no heart body (implied) (Malaquin 1893: 264).

Chaetal structures. 105–124. Chaetae. Aciculae, dentate compounds with a single ligament, and capillary chaetae are present.

Terebellidae. General references: Hessle (1917); Heimler (1978, 1981, 1983); Holthe (1986a,b); McHugh (1995a).

Head structure. 1–4. Prostomium. Heimler (1983: fig. 3) demonstrated that the prostomium of terebellids is reduced and fused to an anterior prolongation of the peristomium.

5–9. Peristomium. Heimler (1983: fig. 3) shows the peristomium as fused with anterior segments and projecting forward from the mouth region. This is interpreted here to represent extended lips.

13–24. Palps. Terebellid tentacles are hypothesised here to palpal in nature and as emerging prostomially, based on positional relationships in the juveniles (Heimler 1978,1983: fig. 3). This requires further investigation.

25–28. Nuchal organs. Present, though absent presumed lost or indistinct in some taxa (Heimler 1983: fig. 3; Rullier 1951: 280–283). Not uniformly absent in the Amphitritinae and Polycirrinae as implied by McHugh (1995a).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands are present (Storch 1968: fig. 26).

31–43. First segment structure and appendages. First segment is fused to the peristomium. Fauvel (1927: 241) stated that (noto) chaetae first are present from segment 2, that is the first branchiferous segment, in larvae "while they disappear from the second or the third segment in adult amphitritins, and are present from segment 3 in adult *Thelepus* and from segment 2 in (adult) *Streblosoma*". Fauvel's statement implies that there is at least one achaetigerous (though branchiferous) segment present in adult terebellids (see also Heimler 1983: fig. 3).

44–55. Parapodial structures. Tori are present (Heimler 1981: figs 47–51).

56–59. Gills or branchiae. Scored as dorsally branching. They are absent in one subfamily, the Polycirrinae and in several genera of Amphitritinae. Amphitritin branchiae usually distinctly stalked and branched, but the stalk may be short, and the branchial filaments appear as groups emerging from the dorsum as is the case in the Thelepodinae (Fauvel 1927: 240). Even though the Polycirrinae are the plesiomorphic terebellid 'clade' in McHugh (1995a), consideration of the fact that branchiae are present in the trichobranchids suggests that the absence of branchiae is a loss in polycirrins.

Digestive system. 78–83. Ventral pharynges and associated structures. A non-eversible ventral buccal organ is present in terebellids (Sutton 1957: 493, fig. 2; Dales 1963). Sutton (1957: 503–505) indicated that the lips,

especially the upper lip, manipulated food, but the pharynx is not eversible.

84–88. Gular membrane and gut. A gular membrane is present (Meyer 1887; Hessle 1917: 57–58; Sutton 1957: 504). The gut is straight in some taxa (Sutton 1957), but distinctly looped in others (Wirén 1883: 31–32, pl. 6, figs 1–3). The latter condition is scored as present.

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia as mixonephridia according to Goodrich (1945: 192–193). Smith (1988) argued that terebellids should have what is termed metanephromixia, but this cannot be accepted since the condition seen in terebellids is not similar to the metanephromixia of the Syllidae, Hesionidae, etc. They are clearly more similar to those other taxa scored with mixonephridia (e.g. Pectinariidae, Serpulidae and Sabellariidae). The issue deserves much further investigation, and the current classification is clearly unsatisfactory, but coding the Terebellidae with metanephromixia is clearly wrong (see Discussion).

96–99. Organisation/distribution of segmental organs. Restricted to a few pairs anteriorly with the foremost being excretory only (Goodrich 1945: 192–193; Hessle 1917; Meyer 1887: 634; Smith 1988).

100. Sperm morphology. No mitochondrial interpolation (Rouse & McHugh 1994).

Circulation. 101–104. Circulation and heart body. Closed circulation with a heart body (Meyer 1887; Picton 1899; Kennedy & Dales 1958).

Chaetal structures. 105–124. Chaetae. Capillary chaetae and uncini are present.

Tomopteridae. General reference: Åkesson (1962).

Head structure. 1–4. Prostomium. Fused and distinct (Åkesson 1962; fig. 30).

5–9. Peristomium. Limited to lips (Åkesson 1962; fig. 30).

13–24. Palps. The 'prostomial tentacles' of Uschakov (1955: 109) or 'divergent antennae' of Day (1967: 196) are more similar to palps than to antennae (Åkesson 1962: 192–193).

25–28. Nuchal organs. Present (Rullier 1951: 309; Åkesson 1962: 178–179, fig. 28).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. Åkesson (1962) demonstrated that the 'tentacular cirri' of the tomopterids represent parapodial development in the first two segments. During larval development, the first segment is no smaller than other segments, but reduces and finally incorporates with the head. The second segment and its cirri form the first visible segment in the adults.

44–55. Parapodial structures. Åkesson (1962: 166–167, fig. 20) demonstrated that the two oar-shaped pinnae of the parapodia represent the noto- and neuropodia, respectively. Cirri are absent.

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. An unarmed pharynx is present (Dales 1962: 397, fig. 4D).

84–88. Gular membrane and gut. Åkesson (1962: 190) referred to the coelom as being 'non-segmented'; implying the absence of a gular membrane. The gut is straight (Hachfeld 1926: 162).

Excretory/reproductive system. 89–95. Nephridial structures. Protonephridia as protonephromixia (Goodrich 1945: 158–160).

96–99. Organisation/distribution of segmental organs. Along the body (Goodrich 1945: 158–160).

100. Sperm morphology. Mitochondria not interpolated (Franzén 1982).

Circulation. 101–104. Circulation and heart body. Circulatory system is absent (Smith & Ruppert 1988: table 14).

Chaetal structures. 105–124. Chaetae. Aciculae only are present in one or two anterior chaetigers.

Trichobranchidae. General references: Hessle (1917); Holthe (1986a,b).

Head structure. 1–4. Prostomium. Similar to terebellids, fused to an anterior extension of the peristomium and reduced (Holthe 1986b: 164, fig. 78a–c).

5–9. Peristomium. The peristomium is fused with anterior segments and projecting forward from the mouth region (Day 1967: fig. 36.1; Holthe 1986b). Interpreted here that this represents extended lips as in the Terebellidae.

13–24. Palps. Trichobranchid tentacles are considered to be palpal in nature and emerging prostomially, as for the Terebellidae, based on positional relationships in the juveniles (Heimler 1983: fig. 3). This requires further investigation.

25–28. Nuchal organs. Present in *Trichobranchus* (see McHugh 1995a); assumed that the absence in *Terebellides* (Rullier 1951: 282) is a loss.

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. The anterior end is currently understood to include one segment in front of the first branchiae. Where developed (e.g. *Trichobranchus*), pairs of branchiae on

segments 2, 3 and 4. First notochaetae may be present on segment 3 or not until segment 6.

44–55. Parapodial structures. Tori are present (Hessle 1917; Holthe 1986b).

56–59. Gills or branchiae. Up to three pairs of branchiae on succeeding segments present. More than single filaments are present on each segment in most cases (Holthe 1986b: 164).

Digestive system. 78–83. Ventral pharynges and associated structures. A non-eversible ventral buccal organ is present (Wirén 1885: pl. 3, fig. 5, marked B).

84–88. Gular membrane and gut. A gular membrane is present; the gut is looped (Wirén 1885: pl. 3, fig. 5; Meyer 1887: 634).

Excretory/reproductive system. 89–95. Nephridial structures. Metanephridia are present, though the organisation is unknown (Hessle 1917: 131).

96–99. Organisation/distribution of segmental organs. Restricted to a few pairs anteriorly, with the foremost being excretory only (Meyer 1887: 634).

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Wirén (1885, pl. 6, fig. 3) illustrated the central circulatory system in such a fashion that a heart body appears to be present.

Chaetal structures. 105–124. Chaetae. Capillaries, dentate hooks and uncini are present.

Trochochaetidae. General references: Orrhage (1964); Pettibone (1976).

Head structure. 1–4. Prostomium. Distinct groove (Pettibone 1976: fig. 1d).

5–9. Peristomium. Limited to lips (Pettibone 1976: fig. 1b).

10–12. Antennae. A median antenna is present in some forms (Pettibone 1976: 3) and is coded as present here.

13–24. Palps. A pair of peristomial grooved palps is present (Orrhage 1964; Pettibone 1976: fig. 1d).

25–28. Nuchal organs. Present extended (Söderström 1920: 113, fig. 101; Orrhage 1964; Pettibone 1976).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands present (Orrhage 1964: pl. 11, figs 4–6).

31–43. First segment structure and appendages. First segment is similar with similar appendages to following segments (Pettibone 1976: fig. 1).

44–55. Parapodial structures. Parapodia are spioniform with no cirri (Pettibone 1976: fig. 2).

60–65. Sensory structures, papillae and pygidial cirri. Lateral organs are present (Orrhage 1964: 361–362). Pygidial cirri present, multiple (Pettibone 1976: fig. 1h).

Digestive system. 66–72. Stomodaeum. A buccal organ is absent in trochochaetids, presumed lost by Orrhage (1964: 397). The pharynx is clearly eversible (see Pettibone 1976: fig. 1b). The interpretation of the organ as a simple axial proboscis by Purschke & Tzetlin (1996: table 2) is accepted here, but further investigation is required.

84–88. Gular membrane and gut. Unknown.

Excretory/reproductive system. 89–95. Nephridial structures. Orrhage (1964: pl. 11, figs 4–6) shows what appears to be metanephridia. The issue of whether they form metanephromixia or mixonephridia is unresolved (see Spionidae, Poecilochaetidae).

96–99. Organisation/distribution of segmental organs. The discussion by Orrhage (1964: 376–378) implies a similar distribution of gonoducts in the trochochaetids to other spiomorphs.

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. Unknown.

Chaetal structures. 105–124. Chaetae. Capillary chaetae and spines.

Typhloscolecidae. General references: Uschakov (1955, 1972); Day (1967).

Head structure. 1–4. Prostomium. Distinct groove (Day 1967: fig. 9.1d).

5–9. Peristomium. Limited to lips (Uschakov 1955: 112, fig. 14).

10–12. Antennae. Two of the three genera have a median antenna, called dorsal caruncle by Day (1967: 207).

13–24. Palps. Scored absent, a 'palpode' is present (Day 1967: 207), but the homology with palps has yet to be demonstrated.

25–28. Nuchal organs. Present (Uschakov 1955: 112; Day 1967: 207).

Trunk structures. 29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segment indistinct and bears tentacular cirri (foliaceous).

44–55. Parapodial structures. Biramous, with projecting neuropodia and foliaceous dorsal and ventral cirri (Day 1967: fig. 9.1).

56–59. Gills or branchiae. Absent

60–65. Sensory structures, papillae and pygidial cirri. A pair of pygidial cirri is present.

Digestive system. 73–77. Axial muscular pharynx, jaws and other structures. Jaws are absent (see Dales 1962: 397).

84–88. Gular membrane and gut. Unknown.

Excretory/reproductive system. 89–95. Nephridial structures. Protone-

phridia are present (Smith & Ruppert 1988: 234, 235). Other details are unknown.

100. Sperm morphology. Unknown.

Circulation. 101–104. Circulation and heart body. A limited circulatory system is present (Smith & Ruppert 1988: 234).

Chaetal structures. 105–124. Chaetae. Aciculae and capillaries are present.

Uncispionidae. General reference: Green (1982).

Head structure. 1–4. Prostomium. Distinct groove (Green 1982: fig. 1a–c).

5–9. Peristomium. Limited to lips (Green 1982: fig. 1a–c).

10–12. Antennae. A median antenna is present (Green 1982: fig. 1a–c).

13–24. Palps. A pair of peristomial grooved palps is present (Green 1982: 530).

25–28. Nuchal organs. Unknown.

Trunk structures.

29–30. Segmentation and muscle bands. Muscle bands unknown.

31–43. First segment structure and appendages. First segment is similar to those following and has similar appendages, though the chaetae are somewhat elongated (Green 1982: fig. 1b).

44–55. Parapodial structures. Parapodia biramous, spioniform (Green 1982: fig. 2).

56–59. Gills or branchiae. Dorsal flattened branchiae are present (Green 1982: fig. 2).

60–65. Sensory structures, papillae and pygidial cirri. Two pairs of pygidial cirri are present (Green 1982: fig. 1d).

Digestive system. 66–72. Stomodaeum. Proboscis an axial sac according to Green (1982: 535–536).

84–88. Gular membrane and gut. Unknown.

Excretory/reproductive system. Unknown.

Circulation. Unknown.

Chaetal structures. 105–124. Chaetae. Capillaries and dentate hooks are present.

Appendix V

Classification of polychaete families

Based on Fig. 74 and incorporation of taxa excluded from restricted analyses, based on arguments in text. Note that families are listed in alphabetical order under clade names and further information about possible relationships within clades is contained in trees available in the text.

Polychaeta
  Scolecida
    Arenicolidae, Capitellidae, Maldanidae, Cossuridae, Opheliidae, Orbiniidae, Paraonidae, Questidae, Scalibregmatidae
  Palpata
    Aciculata
      Eunicida
        Amphinomidae, Diurodrilidae, Dorvilleidae, Eunicidae, Euphrosinidae, Hartmaniellidae, Histriobdellidae, Lumbrineridae, Oenonidae, Onuphidae
      Phyllodocida
        Acoetidae, Alciopidae, Aphroditidae, Chrysopetalidae, Eulepethidae, Glyceridae, Goniadidae, Hesionidae, Ichthyotomidae, Iospilidae, Lacydoniidae, Lopadorhynchidae, Myzostomidae, Nautillienellidae, Nephtyidae, Nereididae, Paralacydoniidae, Pholoidae, Phyllodocidae, Pilargidae, Pisionidae, Polynoidae, Pontodoridae, Sigalionidae, Sphaerodoridae, Syllidae, Typhloscolecidae, Tomopteridae
      Aciculata *incertae sedis*
        Aberrantidae, Nerillidae, Spintheridae

    Canalipalpata
      Oweniidae, Siboglinidae
      Sabellidae
      Sabellariidae, Serpulidae
      Spionida
        Apistobranchidae, Chaetopteridae, Longosomatidae, Magelonidae, Poecilochaetidae, Spionidae, Trochochaetidae, Uncispionidae
      Terebellida
        Acrocirridae, Alvinellidae, Ampharetidae, Cirratulidae, Ctenodrilidae, Fauveliopsidae, Flabelligeridae, Pectinariidae, Poeobiidae, Sternaspidae, Terebellidae, Trichobranchidae
      Canalipalpata *incertae sedis*
        Polygordiidae, Protodrilidae, Protodriloididae, Saccocirridae
  Polychaeta *incertae sedis*
    Aeolosomatidae, Potamodrilidae, Parerogodrilidae, Psammodrilidae